The foraging ecology of the short-tailed shearwater (*Ardenna tenuirostris*): Life-history strategies and climate change

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Statement of ethical conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University. All animal handling and instrumentation was carried-out under Research Permits, Department of Primary Industries, Parks, Water and Environment (FA05151, FA10212, FA13009, FA14063, FA15083, FA16077) and University of Tasmania Ethics Committee permits (A8138, A11338, A128942, A15572).

ABSTRACT

Climate induced variability of prey abundance and its' distribution, is a dominant factor regulating marine predator lifetime reproductive success and population viability. Seabirds are long-lived and they have evolved life-history traits such as delayed sexual maturity and intermittent breeding that buffer them against environmental variability. However, some species that have restricted dietary and range niches may be more sensitive to persistent negative climate perturbations. Therefore, gaining an understanding of how climate variability affects foraging ecology and reproductive parameters will be imperative if we are to determine the viability of seabird populations into the future. Doing so is important given the predictions that the Earth's climate will continue to change at an accelerated rate in the coming century.

This thesis investigated whether the short-tailed shearwater (*Ardenna tenuirostris*), an abundant seabird of the Southern Ocean, will be resilient in a rapidly changing environment. The foraging behaviour of short-tailed shearwaters from Wedge Island, Tasmania, was assessed over five years (2010 - 2016), and the trophic position of adults during the breeding season was also quantified (2005 - 2008 & 2012 - 2015) as were breeding parameters; breeding effort and success (2004 - 2016). This thesis aimed to 1) examine the non-breeding movements of short-tailed shearwaters and assess within-season foraging plasticity; 2) determine the influence of climate on the trophic position of adults during the breeding season; and 3) assess foraging movements in relation to environmental variability and whether this influenced breeding participation and success, and the mass of fledglings.

(1) Post-breeding, birds selected foraging sites in distinct regions of the Northern Hemisphere, the Sea of Okhotsk/North Pacific Ocean, and the southeast Bering Sea/North Pacific Ocean. Birds spent between 15% and 99% (62.8 ± 20) of the non-breeding season in these core foraging areas. An additional late season foraging region in the Chukchi Sea was utilised by 50% of tracked individuals. Birds that were tracked for consecutive winters (n = 8) returned to the same core foraging site, but the time they spent there varied between years. Having a

hierarchical strategy, where individuals return to familiar areas but disperse when environmental conditions deteriorate would allow short-tailed shearwaters to buffer some of the effects that climate variability has on the distribution and abundance of prey. This is important as environmental conditions (sea surface temperature and sea surface height) vary between regions within and among years; and these regions are undergoing protracted change. Consequently, foraging flexibility may allow short-tailed shearwaters to better adapt to climate induced environmental change.

(2) The trophic level of short-tailed shearwaters during the breeding season was determined using two complimentary techniques, bulk stable isotope analysis (SIA) and compound specific stable isotope analysis of amino acids (AA-CSIA). While there were consistent seasonal trends in the feeding zones birds used within the Southern Ocean, there was little variability in the trophic position of the prey adults consumed during long-trips within or among years.

(3) The foraging movements of breeding birds were examined during both chick provisioning trips (short-trips) and when adults undertook extended trips into the Southern Ocean (long-trips). Whilst provisioning chicks, adults foraged within the shallow continental waters surrounding Wedge Island but undertook extended multi-day trips within the Southern Ocean when self-provisioning. When the Southern Annular Mode (SAM) was negative, adults travelled further and spent less time foraging, most likely because primary productivity was supressed in the regions, which birds travelled to during long-trips. Both the number of birds that engaged in breeding activities and breeding success varied considerably during the study period. Interestingly, climate variability was not found to influence the number of birds that bred, or breeding success. However, chicks fledged with lighter body masses when local sea surface temperature was warmer and when the SAM was positive. Such conditions could cause change in the distribution and abundance of the prey, which probably reduces the amount of energy chicks receive, resulting in reduced body mass at fledging.

By integrating information on the foraging distribution of short-tailed shearwaters throughout the annual cycle, in addition to the analysis of trends in the trophic level of prey consumed by breeding adults and the incorporation of intrinsic rates of breeding participation and success, this thesis provides important insights into how this abundant seabird deals with change in the distribution and availability of its resources. By having an extended foraging range and a flexible foraging strategy means that this species can better deal with changes in the environment compared to seabirds that have a restricted foraging range and narrow dietary niche. Nonetheless, the change in the functioning of the marine environment has the potential to reduce the size of short-tailed shearwater populations by increasing the rate of intermittent breeding and by reducing chick survival post-fledging.

Statement of chapter contributions

This thesis contains three manuscripts in preparation for submission to peer-reviewed journals. Natalie Bool was responsible for data collection during 2012 to 2016, data analysis, interpretation and preparation of all manuscripts and some laboratory analyses in this thesis.

The following people and institutions contributed to the preparation of work undertaken as part of this thesis:

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Associate Professor Mary-Anne Lea (Institute for Marine and Antarctic Studies) –
Candidate supervisor
Dr Clive McMahon (Sydney Institute of Marine Science) – Candidate supervisor
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Chapter Three: Bool, N. (68%), Vertigan, C. (5%), Revill, A. (5%), Lea, M.A. (5 %), McMahon, C. (5%), Daniel, O.D. (2%), Hindell, M.A. (10 %)

Chapter Four: Bool, N.M. (65%), Cleeland, J. (5%), Sumner, M.D. (5%), Lea, M.A. (5%), McMahon, C. (5%), Vertigan, C. (5%), Hindell, M.A. (10%)

Details of authorship

Chapter 2: Prof. Mark Hindell contributed to data interpretation and analyses and manuscript preparation. Asoc. Prof Mary-Anne Lea and Dr Clive McMahon contributed to the discussion and critical evaluation of the manuscript. Dr Michael Sumner assisted with visual presentation of foraging data and he helped acquire environmental data for analyses.

Chapter 3: Dr Caitlin Vertigan contributed stable isotope data collected from short-tailed shearwaters in 2005 to 2007. Owen Daniel contributed stable isotope data collected from short-tailed shearwaters in 2008. Prof. Mark Hindell contributed to data interpretation and analyses and manuscript preparation. Dr Andy Revill carried-out compound stable isotope analyses and he provided technical advice. Assoc. Prof Mary-Anne Lea and Dr Clive McMahon contributed to the discussion and critical evaluation of the manuscript.

Chapter 4: Dr Jaimie Cleeland contributed foraging data collected from short-tailed shearwaters in 2010. Dr Caitlin Vertigan collected and collated the Wegde Island population census data between 2004 to 2010. Prof. Mark Hindell contributed to data interpretation and analyses and manuscript preparation. Assoc. Prof Mary-Anne Lea and Dr Clive McMahon contributed to the discussion and critical evaluation of the manuscript. Dr Michael Sumner assisted with visual presentation of foraging data and helped to acquire environmental data for analyses.

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Professor Mark A. Hindell
(Candidate's Supervisor)

Professor Craig Johnson
(Head of Centre – Ecology and Biodiversity)

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CHAPTER 1 GENERAL INTRODUCTION

Climate change is having pervasive effects on animal populations by causing changes in the timing, distribution and abundance of food resources (Parmesan, 2006). How resilient animal populations are to these shifts will be influenced by species-specific habitat niche breadth (restricted or diverse), dietary niche width (specialist or generalist), and also life-history traits (e.g. fecundity and life-span), dispersal capability and behavioural plasticity (Cayuela et al., 2017, Jiguet et al., 2007, Parmesan, 2006, Williams et al., 2008). Those species which have a restricted range and a specialist diet, especially those that live at high altitudes and latitudes, are considered to be more sensitive to climate mediated changes (Jiguet et al., 2007, Parmesan, 2006). Conversely, increasing global temperatures are allowing a wide array of taxa to expand their range pole-wards and to higher elevations (Hickling et al., 2006, Moritz et al., 2008). Thus, not all animal populations will be negatively affected by environmental change. Therefore, to gain a better understanding of how animal populations will be influenced by climate change; information on foraging ranges, dietary niches and life-history characteristics needs to be collected from a wide diversity of taxa.

Life-history trade-offs, adaptations and constraints

The likelihood of animals adapting to rapid climate change will in part be related to species specific generation times and the ability to reproduce viable offspring in modified environments. Reproduction is costly for wildlife; consequently, animals must make fitness trade-offs (Stearns, 1989, Williams, 1966). This can involve allocating time and energy to producing offspring when conditions are favourable, or channelling energy into self-maintenance when food availability is limited (Lack, 1954). Such decisions are largely determined by species-specific life-history characteristics, as the trade-off between the time and energy that can be invested into growth, maintenance and the current reproductive effort compared to present and long-term survival depends on heritable traits such as generation time and fecundity (Nylin and Gotthard, 1998). The life-history strategies of animals are categorised broadly in relation to their reproduction rate and longevity. Animals fall along a continuum of either ‘r’ or ‘K’ selected species (Figure 1.1) (Putman and Wratten, 1988). Species which evolved to produce a few slow maturing offspring that require considerable parental care are ‘K selected’ (Putman and Wratten, 1988). These organisms live in stable habitats (at least over the long-term), which favour a long lifetime, allowing their populations to persist near, or at, carrying capacity (Odum and Barrett, 2005, Williams, 2013). Investment in growth and maintenance are priorities for long-lived species where competition for

resources is high between conspecifics. Hence, when resources are scarce, they may opt not to breed, thus maximising the adults' survival chances and future reproductive output. In contrast, 'r' selected organisms are short-lived, produce many young which develop quickly and require little parental input (Promislow and Harvey, 1990). These adaptions allow r-selected populations to grow exponentially in seasonally temporary environments, and to quickly establish new territories in disturbed and adjoining habitats (Williams et al., 2010). Consequently, these groups of animals may respond to directional climate change in vastly different ways.

Changing global temperatures and weather patterns are causing the timing of resource availability to change (Bradley et al., 1999b, Dunne et al., 2003, Edwards and Richardson, 2004, Thackeray et al., 2010). Animals that are reliant on the seasonal availability of resources for reproduction may need to adjust the timing of reproduction and other life events, such as migration, in order to better cope with a changing climate (Both et al., 2009, Travis et al., 2013). For example, populations of r-selected species, such as rats and mice, have short gestation and generation times. This means that their populations can quickly grow when resources become available, which may make them more suited to a changing climate (Bronson, 2009), whereas the fitness and reproductive success of some species is tightly linked with the seasonal availability of resources. For example, the mass and the number of fledglings of great tits (*Parus major*) decreased over a 20 year period because of an increasing mismatch in the timing of food resources (peak caterpillar biomass) and when the birds commenced breeding (Visser et al., 2006). Trophic mismatches in the timing of resource availability can reduce breeding success and cause population decline (Møller et al., 2008, Post and Forchhammer, 2008, Winder and Schindler, 2004). There is considerable evidence indicating that a range of taxa will not be able to adapt fast enough as they are reliant on seasonal food peaks and because they have a restricted period of time in which to produce offspring (Bronson, 2009, Burthe et al., 2012, Inouye et al., 2000, Nussey et al., 2005, Thackeray et al., 2010).

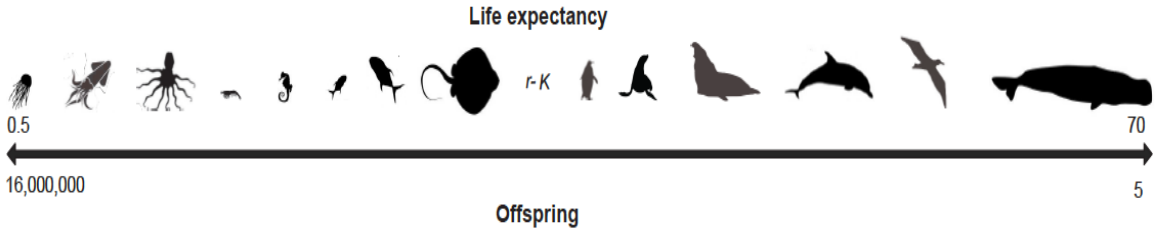

Figure 1.1. Example of r-K marine species. r-selected species (left) and K-selected species (right) indicated above the line. Scale is non-linear and life expectancy (years) and the number of offspring shown below the line are approximate and are presented for illustration purposes only.

Range expansion and resource use as mechanisms for adaptation

Dispersal capabilities and diet breadth are also thought to be important factors that contribute to the extent that animals can adapt to climate change. Being specialised, i.e. using a restricted subset of the total resources available, may decrease the capacity of some species to adapt to rapid climate change over short time scales (Colles et al., 2009, Slatyer et al., 2013). Localised declines in resources could have more pronounced effects on species, which have small ranges, especially those that have a narrow dietary niche (Polato et al., 2018, Urban et al., 2012). For example, coral reef bleaching causes the loss of resources for reef fishes and this results in higher rates of decline in specialist fishes, in particular those that have small populations (Munday, 2004). In contrast, generalist species that use a wider array of resources, have short generation times and which are highly mobile may be better able to adapt to change in their environment (Bhagwat and Willis, 2008). Although, a change in diet may not be necessary for species which have large home-ranges, such as baleen whales, as moving to areas where prey is more abundant may increase food intake when resources are limited (Nicol et al., 2008). However, the success of this strategy will be dependent on increased energy gains in the new foraging areas. In some cases, inter-specific competition for prey and predation may prevent successful range expansion and colonisation of new habitats (Case et al., 2005, Holt and Barfield, 2009). Overall, it is challenging to predict how animal populations will respond to directional climate change and whether dispersal and diversifying resource use will pay off, as there is a multitude of interacting factors that act upon animal populations.

Seabird life-history adaptations in a changing climate

Climate induced variability of prey abundance and its distribution is a dominant factor regulating marine predator lifetime reproductive fitness and population viability. Large-scale atmospheric climate circulations are closely coupled with ocean productivity and these have the potential to affect seabirds at local and basin wide scales (Barbraud and Weimerskirch, 2003, Barrett and Erikstad, 2013, Sandvik et al., 2008). Seabirds, as a group, display diverse physiological and life-history traits, which evolved for a life in the marine environment where prey availability is temporally variable and patchily distributed (Weimerskirch, 2007).

To procure patchily distributed food in a competitive environment, seabirds evolved differing morphological and behavioural adaptations (Catry et al., 2013, Ricklefs, 1990, Stearns, 1977). These include differences in diet (Croxall and Prince, 1980), specialised adaptations for prey capture (e.g. dive behaviour (Kato et al., 2006)), and the evolution of migration in many species (Alerstam et al., 2003, Fort et al., 2013). Such adaptations are seen in penguins which cannot fly and auks which have reduced flight ability in favour of better diving performance (Elliott et al., 2013). In comparison, albatrosses, petrels and shearwaters have a number of physical adaptations that allow them to minimise the costs of flying and subsequently they can search for prey over great distances (Warham, 1977, Weimerskirch et al., 2000). Further, some seabirds have a generalist diet; giant petrels (*Macronectes spp.*) (González-Solís et al., 2000) and kelp gulls (*Larus dominicanus)* (Favero and Silva, 1997) scavenge on carrion and also obtain food from the ocean, known as type A generalists (Bearhop et al., 2004),whereas type B generalist populations are composed of individual specialists with a narrow dietary niche. For example, at the population level thick-billed murres (*Una lomvia)* consume a wide array of prey, but individuals are specialised (Hamish et al., 2009). Within a population, the partitioning of resources between conspecifics would increase individual foraging success by reducing intra-specific competition and such behaviour would also buffer the population against decline in any single food type (Bolnick et al., 2003, Ceia and Ramos, 2015).

In contrast, specialist seabird populations that have a narrow dietary niche may be less able to cope with a rapidly changing climate than those that have a generalist diet (Forcada and Trathan, 2009, Gremillet and Boulinier, 2009, Jenouvrier et al., 2014, Joiris, 2017). For example, black-legged kittiwakes (*Rissa tridactyla*) are considered to be particularly

vulnerable to food decline as their populations are often dependent on the availability of a single fish species and they appear to be limited in their capacity to switch to alternative prey (Barrett, 2007). Further, when the principal prey of least auklets (*Aethia pusilla*), copepods, are in low abundance these birds experience nutritional stress (Dorresteijn et al., 2012) and chick growth and survival is reduced (Gall et al., 2006). Given that seabirds display a broad range of behavioural and physiological traits, highlights the need to undertake research to better understand how this diverse taxonomic group will fare into the future.

Monitoring seabird populations

Despite the physiological and behavioural differences of seabirds, they broadly share a number of life-history strategies; they are typically long-lived, have low reproductive rates and delayed sexual maturity, and chicks develop slowly (Ricklefs, 1990). To understand how climate change may affect seabird populations, a number of *vital* rates, e.g., annual variability of breeding effort, reproductive success, foraging distribution and diet can be monitored (e.g. Cubaynes et al., 2011, Frederiksen et al., 2012, Horswill et al., 2017, Kitaysky et al., 2006). Measuring breeding chronology and chick condition is particularly important as variability in these intrinsic rates provides an indication of how climate influences seabird populations more quickly than can be found through monitoring population size trends in these long-lived animals (Chambers et al., 2015). In addition, breeding success will show among year variability more readily than adult survival, as adults are more likely to ensure their survival over that of their offspring (Barbraud et al., 2011).

Underpinning the mechanistic links between foraging ecology (where and how seabirds find their food) will also provide greater insight into how climate change influences seabird populations (Morales et al., 2010). This is particularly important because responses of seabirds to climate variability will differ dependent on species-specific life-history traits, dietary niches and dispersal capabilities (Barbraud et al., 2011, Kitaysky and Golubova, 2000, Sandvik and Erikstad, 2008). Therefore, to identify how seabirds are affected by increasing global temperatures (Parmesan and Yohe, 2003, Pörtner et al., 2014) will require knowledge of how they distribute themselves, what they eat and how variability of these metrics influences reproductive output (Gremillet and Boulinier, 2009).

Foraging ecology

The availability of prey within foraging distance of land-based nests is necessary for successful breeding in central-place foragers, such as seabirds. Therefore, seabirds must balance the distance they travel to find prey with the need to provision young (Orians and Pearson, 1979). Nutrient poor waters surrounding colonies and intra- and inter-specific competition are thought to have contributed to the evolution of bi-modal foraging in seabirds, which is widespread in Diomedeidae and Procellariidae during the breeding season (Baduini and Hyrenbach, 2003, Congdon et al., 2005, Welcker et al., 2012, Welcker et al., 2009). These seabirds alternate between short-trips in areas surrounding the colony to provision their chicks, and distant long-trips to replenish lost reserves (Chaurand and Weimerskirch, 1994, Weimerskirch et al., 1994). During short-trips to provision chicks, adults lose condition as prey is not assimilated (Weimerskirch, 1998). This presents a trade-off between the current reproductive effort of an adult bird and its long-term fitness, as the time spent foraging for self-maintenance influences the timing and frequency of prey fed to chicks (Chivers et al., 2012). Long-lived seabirds maximise their lifetime reproductive success by maintaining high adult survival, but this can come at a cost to their current reproductive effort if energy and resources are directed towards self-maintenance (Schultner et al., 2013). Nonetheless, over the lifetime of an individual, it should have many opportunities to successfully raise offspring under more favourable conditions.

Although seabirds are not burdened by the need to return to land-based nests during the non-breeding stage, they need to recover energy reserves lost whilst engaged in breeding activities and they also need to store energy for future reproductive efforts (Daunt et al., 2006, Sorensen et al., 2009). Stochastic climate events can diminish prey availability in non-breeding staging areas, which can reduce the capacity of birds to commence breeding activities and also lower adult survival (Baduini et al., 2001a, Barbraud and Weimerskirch, 2003). Regardless of the stage of the annual cycle a close connection between environmental variability, e.g. fluctuating sea surface temperature, water thermal structure, wind strength and ocean productivity have been found to influence seabird foraging behaviour (Carroll et al., 2016, Einoder et al., 2013, Kokubun et al., 2010, Weimerskirch et al., 2012, Wilson et al., 2002). Therefore by incorporating information on the foraging distribution of seabirds throughout the annual cycle, i.e. both the breeding and non-breeding stages, will strengthen understanding of how seabird populations respond to climate variability.

Monitoring foraging behaviour

To address the question of where animals find their prey, a number of tracking devices were developed and are now extensively used by seabird ecologists (Wilson and Vandenabeele, 2012). VHF (Very High Frequency) telemetry, GPS (Global Position System), GLS (Global Location Sensors) and PTT (Platform Terminal Transmitters) can be easily attached to seabirds (Wilson et al., 2002). These devices provide varying levels of information regarding foraging metrics. GLS loggers record light levels, which is used to estimate day length, based on when sunrise and sunset twilights occurred and this can be used to coarsely calculate longitude and latitude of the animal at these times (Hill, 1994). Some GLS are capable of recording SST, which can be cross-referenced with light data to provide more accurate location estimates and some devices also record periods of wet and dry which can be interpolated to indicate activity levels (whether the animal was in the water or either flying or sitting on land) (Shaffer et al., 2005, Wotherspoon et al., 2013). In contrast, GPS loggers can provide frequent precise (~ 4 m accuracy) location estimates but these devices are heavier, have battery constraints and can perform poorly when the animal is submerged (Burger and Shaffer, 2008).

When seabird foraging locations are integrated with environmental covariates such as sea surface temperature (SST) and chlorophyll *a* (measures of ocean productivity), they provide a platform to better understand how seabird movements relate to environmental variability (Jonsen et al., 2013). Therefore, both GLS and GPS captured location data have provided considerable insight into how foraging behaviour is influenced by environmental variability and how this influences breeding success and population trends (Bestley et al., 2016, Wakefield et al., 2009).

The importance of monitoring seabird diet

The quality and abundance of seabird prey influences the energy adults can commit to raise their offspring, whilst also determining the rate of growth, development and size of chicks at fledging (Gonzalez-Medina et al., 2017, Kadin et al., 2016). Ultimately, chicks that are heavier have a greater chance of survival post-fledging (Kitaysky et al., 2006, Sagar and Horning, 1998). Thereby, documenting the responses of seabirds to the spatial heterogeneity of their prey can be determined by monitoring their diet, as this can reflect changes in prey

assemblages and abundance which can then be linked to broad-scale atmospheric processes that underpin the relationship between predators and their food resources.

There are many methods, which are used to identify the prey consumed by seabirds. These include stomach regurgitations (obtained from stomach flushing), extracting DNA from excrement, collection of regurgitated pellets, and through direct observation of prey returned to the colony (although more suited to alcids, etc.) (Barrett et al., 2007). However, it is not possible to determine the diet of seabirds that spend extended periods of time at sea using these methods alone (Cherel et al., 2000, Lorrain et al., 2009, McInnes et al., 2016). Seabird diet studies that use prey obtained from stomach samples during the breeding season are also constrained as this only reflects what is fed to chicks and does not incorporate the food that is consumed to maintain the adults' body condition (Barrett et al., 2007, Cherel et al., 2005b, Weimerskirch and Cherel, 1998). Further, prey collected from stomach samples typically undergoes digestion prior to collection, which can bias results (Bowen and Iverson, 2013). Consequently, alternative methods such as fatty acid analysis and stable isotope analysis (SIA) are increasingly used to monitor seabird diet as these can be used to identify long-term trends (Connan et al., 2007, Watanuki and Thiebot, 2018). Fatty acid analysis can identify species without hard parts and indicates relative proportions of prey consumed (Budge et al., 2006, Iverson et al., 2004), although this method is reliant on a priori information of the fatty acid signatures of seabird prey (Iverson et al., 2004). Whereas stable isotope analysis (SIA) is used to determine the trophic position of seabirds and their prey, and it also provides an indication of the prey source (Bond and Jones, 2009).

Monitoring trends in food availability using stable isotope analysis

Bulk SIA is used to assess trends in animal diets as these isotopes behave in a predictable manner (Bond and Lavers, 2014, Ciancio et al., 2015, Granadeiro et al., 2014, Lajtha and Michener, 1994). The measurement of natural isotope abundances of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in proteins allows the dependence of animals on prey and habitat types to be determined (Bond and Jones, 2009). The ratio of the heavy to light isotopes of these elements can be measured relatively easily using an isotope mass spectrometer (Fry, 2006). Mass spectrometer measurements can be compared to international standards to provide an indication of the trophic source of food consumed by seabirds. Carbon ($\delta^{13}C$) in plants and

animals is lighter than the Pee Dee Belemnite standard, these values are subsequently negative, whereas nitrogen ($\delta^{15}N$) values are positive as plant and animal tissues are heavier than the standard (atmospheric nitrogen) (Fry, 2006).

The ratio of carbon isotopes in the diet is used to infer the geographic location of where the organism obtained its resources as $\delta^{13}C$ is only slightly enriched (1-2‰) in consumers compared to the source, reducing its use to infer trophic position (Kelly, 2000). Phytoplankton has lighter $\delta^{13}C$ than inshore plants, and this difference is used to determine onshore versus offshore foraging in marine organisms (Kelly, 2000, Ramos and Gonzalez-Solis, 2012). Carbon in phytoplankton also becomes depleted in high latitudes due to seasonally low photosynthetic rates, which can be detected along gradients associated with latitude (Goericke and Fry, 1994, Rau et al., 1982). In the Southern Ocean, marine mammal and seabird $\delta^{13}C$ ratios are correlated with latitude (Cherel and Hobson, 2007). However, this trend is not universal, $\delta^{13}C$ was a poor predictor of geographic variability of Procellariiformes in the mid-northeast Atlantic (Roscales et al., 2011).

Although it is difficult to determine the exact prey composition of seabird diets using bulk SIA, it is possible to estimate their trophic position, using $\delta^{15}N$. The stable isotopic signatures of prey consumed are detectable in body tissues (blood, feathers, bones, organs) (Bearhop et al., 2004). During assimilation, ^{14}N is preferentially removed from the diet and ^{15}N is absorbed in the process of utilising amino acids from proteins (Barrett et al., 2007). Through this process, nitrogen becomes enriched by ~3.4‰ in the consumer compared to the diet (Deniro and Epstein, 1981). $\delta^{15}N$ is used to estimate trophic position of predators and their prey, as this enrichment is associated with a trophic step from prey to consumer (Newsome et al., 2010). For example, fish and cephalopods are enriched in $\delta^{15}N$ compared to zooplankton (Morrison et al., 2014).

Stable isotope mixing models can be used to estimate the contribution of different prey to the diet (Cherel et al., 2005a, Phillips and Gregg, 2001, Phillips et al., 2014). However, this is reliant on having a priori isotopic information on the animals' prey, which can be costly and logistically challenging for wide-ranging species. Stable isotope values can also be used to infer the isotopic niche of consumers (Bearhop et al., 2004, Jackson et al., 2011). Estimates of isotopic niche specialisation can be determined by calculating the distribution of stable

isotope values, providing a bi-plot of diet based on paired $\delta^{15}N$ and $\delta^{13}C$ values of an individual or community (Syvaranta et al., 2013). However, the known error associated with the variability of isotopes at the baseline in the marine environment suggests that these methods should be used cautiously when studying wide-ranging seabirds (Newsome et al., 2010).

Baseline variability in source isotopes

Baseline concentrations of ^{15}N vary spatially and temporally in the marine system, and this directly influences trophic enrichment of the food eaten by consumers. For example, seabirds breeding in northern high latitude areas are enriched in $\delta^{15}N$ compared to the same species breeding in tropical areas, presumably because of different baseline levels (Roscales et al., 2011). Gaining estimates of baseline isotopes is difficult, as the assimilation of $\delta^{15}N$ by primary producers can vary temporally due to upwelling (O'Reilly et al., 2002) and bloom events (Tamelander et al., 2009). Such occurrences could result in variability of $\delta^{15}N$ in consumers over time from the same area. Consequently, the assimilation of $\delta^{15}N$ by primary producers varies, which could have implications for estimates of trophic level of prey across large water masses and over time. Currently, very few studies that used SIA to infer trophic trends in seabirds considered the contribution of baseline variability (although see Lorrain et al., 2009, McMahon et al., 2015). Incorporating baseline variability of $\delta^{15}N$ values of wide-ranging seabirds is likely to be particularly important as they can take prey from a range of habitats that could be subject to baseline variability and this could have implications for predator-prey trophic coupling.

In recent years development of compound specific isotope analysis of amino acids (AA-CSIA) has improved the accuracy of determining trophic relationships among predators and their prey (Nielsen et al., 2015). The benefit of the AA-CSIA approach is that it allows differentiation of isotopic values of $\delta^{15}N$ and $\delta^{13}C$ at the base of the food chain, compared to values attributed to the assimilation of prey into the consumers diet (Lorrain et al., 2009, Seminoff et al., 2012). This distinction is a key one as the uptake of $\delta^{15}N$ by organisms at the base of the food web is subject to temporal and spatial variability (Mackey et al., 2015, Nielsen et al., 2015). Some AAs, such as phenylalanine (Phe), do not become enriched in $\delta^{15}N$; instead it retains the $\delta^{15}N$ signature of the source. In contrast, glutamic acid becomes enriched in $\delta^{15}N$ relative to the prey source, and thus provides an estimate of prey tropic

position. Therefore, AA-CSIA compliments bulk stable isotope analysis as it measures the relative input of source $\delta^{15}N$ in the consumer's diet.

Points to consider when using SIA

One of the main limitations of bulk isotope analysis is the calculation of trophic position (TP), which relies on several assumptions about the species assimilation of $\delta^{15}N$ (McMahon and McCarthy, 2016). For example, the differences in the enrichment of isotopes in the consumer is dependent on: the species size (Cabana and Rasmussen, 1996), the tissue used (Pinnegar and Polunin, 1999), species diet (McCutchan et al., 2003), and the water temperature the consumer lives in (Barnes et al., 2007). Consequently, trophic enrichment between prey and the consumer can be species-specific (McCutchan et al., 2003, Post, 2002, Weiss et al., 2009). The use of Trophic Discriminant Factors (TDF) to determine trophic levels of seabirds should be applied with caution as very few studies have been conducted on the assimilation of prey in seabirds (Bond and Jones, 2009); therefore calculating trophic position, assuming that trophic enrichment between prey and consumer is 3.4‰, may lead to inaccurate trophic position estimates.

The turn-over rates of stable isotopes vary between tissues and so the time that the prey eaten by seabirds takes to assimilate into the chosen sample needs to be considered. Isotopes signatures found in feathers incorporate the diet and its source at the time of growth (Hobson and Clark, 1992a), whereas whole blood has a half-life isotopic turnover rate of 12 - 20 days (Barquete et al., 2013, Bearhop et al., 2002, Hobson and Clark, 1993). Toenails and claws have a much slower synthesis (~125 days), reaching equilibrium at the time of toenail replacement (Lourenco et al., 2015), so short- to medium-term diet shifts are not necessarily detectable (Barquete et al., 2013). Stable isotope analysis can provide an indication of the trophic level of prey assimilated over time, allowing for long-term dietary studies without destructive sampling. However, another caveat to be considered is that food synthesis varies between tissues, for example feathers, bone and skin are more enriched in ^{15}N than blood (Cherel et al., 2005a, Hobson and Clark, 1992b, Mizutani et al., 1992, Quillfeldt et al., 2008). Also, lipid content varies between tissues. Lipids in muscle and liver are depleted in ^{13}C and are typically removed from these tissues (Deniro and Epstein, 1977, Kojadinovic et al., 2008, Pinnegar and Polunin, 1999). Whereas lipid removal from blood plasma, on the other hand,

increases $\delta^{13}C$ values, and it is therefore not necessary to extract lipids from blood (Cherel et al., 2005b).

The influence of climate variability on the seabirds of the Southern Ocean

During the past 50 years the Antarctic polar region has undergone rapid regional warming (Meredith and King, 2005, Moline et al., 2008, Stammerjohn et al., 2008a, Vaughan et al., 2003). For example, SST in the Indian and Pacific Ocean sectors has increased in both the mid and top water layers, between 45° and 60° E (Gille, 2002, Jacka and Budd, 1998) in areas associated with the Antarctic Circumpolar Current (ACC). The duration of maximum sea ice extent has decreased by 1 - 3 days between ~95º to 110ºE in association with coastal polynyas, but there are also areas where the sea ice season is longer, primarily between 160° to 170°E (Massom et al., 2013). Such a pronounced warming trend is resulting in ecosystem shifts, extending from krill to higher trophic predators (Ducklow et al., 2007, Smetacek and Nicol, 2005).

The Southern Ocean is estimated to support 69 million pairs of seabirds on sub-Antarctic islands and the Antarctic continent (Riddick et al., 2012). Many other species also depend on the Southern Ocean to find their prey but return to land in areas north of the Southern Ocean to breed (Shirihai, 2002), such as the short-tailed shearwater (*Ardenna tenuirostris*) (~23 million breeding pairs) (Skira et al., 1996) and the sooty shearwater (*Adrenna grisea*) (~20 million individuals) (Brooke, 2004). Seabirds are an important component of the Southern Ocean; where they congregate in large numbers their guano increases phytoplankton growth (Shatova et al., 2017, Wainright et al., 1998), thus contributing to the cycling of nutrients in the Southern Ocean. Seabirds are also major consumers of biomass in this region, reliant on krill as secondary and primary prey, myctophid fish, and squid (Adams et al., 1993, Brooke, 2004, Woehler, 1997, Woehler and Green, 1992). The sheer abundance of seabirds in the Southern Ocean highlights the importance of gaining understanding of how climate variability and change will influence their spatio-temporal foraging ecology and what this means for the sustainability of their populations.

Where data exists a number of clear patterns concerning Southern Ocean seabird population dynamics have been detected; these include reduced adult survival, poor breeding success and intermittent breeding, all of which have been linked to warming temperatures and

reduced sea ice extent (Ballerini et al., 2009, Baylis et al., 2012, Chambers et al., 2014, Descamps et al., 2016, Fay et al., 2015, Forcada et al., 2006, Hindell et al., 2012, Jenouvrier et al., 2005, Trivelpiece et al., 2011, Wilson et al., 2001). For example, Adelie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarcticus)* penguin populations in the Western Antarctic Peninsula and the Scotia Sea have declined due to decreasing Antarctic krill (*Euphausia superba*) stocks which has been linked to competition with recovering whale and seal populations in conjunction with increasing sea surface temperatures (Trivelpiece et al., 2011). Similarly, changes in sea ice dynamics is also influencing emperor penguin (*Aptenodytes forsteri)* adult survival and breeding success, therefore it is projected that by the year 2100 two-thirds of their population will have declined by 50% (Jenouvrier et al., 2014).

It is important to note though that some species appear to be better adapted to change in the Southern Ocean. The wandering albatross (*Diomedea exulans*) (Weimerskirch et al., 2012), has had increased breeding success due to increased polar winds; and reduced sea ice cover has permitted ice tolerant gentoo (*Pygoscelis papua)* and king (*Aptenodytes patagonicus*) penguins to expand their distribution to more southerly extents (Forcada and Trathan, 2009, Peron et al., 2012). Overall, the lack of data on basic biological parameters, like foraging distribution, dietary niches and life-history plasticity, survival, and recruitment makes it difficult to make precise predictions about the viability of many of the seabird populations of the Southern Ocean into the future (Baker et al., 2002, Chambers et al., 2011, Gremillet and Boulinier, 2009).

The short-tailed shearwater (*Ardenna tenuirostris*)

The short-tailed shearwater is a migratory medium sized Procellariiform (~550 g), which is present in the Southern Ocean from September to May (Skira, 1991). Short-tailed shearwaters are the most abundant seabird in Australia with an estimated 23 million pairs breeding at 285 colonies (Skira et al., 1996). This abundant species is ranked fifth highest in global seabird consumption of marine resources and third highest in the Southern Ocean (Brooke, 2004). Their breeding distribution is restricted to southern Australia, with the highest concentration of colonies found in Tasmania (Skira et al., 1996). These seabirds employ a number of life-history adaptations that have contributed to their position as an important pelagic predator of the Southern Ocean. Short-tailed shearwaters live up to 50 years (~35 years), have low adult morality (Bradley et al., 1991, Bradley et al., 1989), produce only one chick per year, and

have delayed onset of breeding (~7 years) (Bradley et al., 1999a). Currently, the species is listed as "Least Concern" by the International Union for Conservation for Nature (IUCN). Although there have not been recent estimates of the population size of short-tailed shearwaters, it appears that there could be widespread decline (BirdLife-International, 2017).

The breeding stages

Short-tailed shearwaters return to the breeding colonies in late September to early October after spending the non-breeding stage in the North Pacific (Skira, 1991). Upon return to the colony, short-tailed shearwaters renovate their burrow, copulate and then undertake an extended pre-laying foraging trip into the Southern Ocean where the birds accumulate energy reserves for breeding (Figure 1.2) (Cleeland et al., 2014). The commencement and cessation of breeding is highly synchronous, the egg is laid during the last week of November (Marshall and Serventy, 1956). Incubation lasts ~53 days and both adults take turns incubating the egg and caring for the chick (Carey, 2011). Short-tailed shearwaters employ a bi-modal foraging strategy during chick rearing, alternating between one to three short local foraging trips (1-2 days) to provision the chick, followed by a long foraging trip (7-32 days) within the Southern Ocean to maintain the adults' body condition (Berlincourt and Arnould, 2015, Cleeland et al., 2014, Einoder et al., 2011, Klomp and Schultz, 2000, Weimerskirch and Cherel, 1998). These long-foraging trips have a dual purpose, as the adults also convert prey into an energy rich oil, which they transport back to the chicks (Oka, 2011). In response, chicks accumulate considerable fat reserves to allow them to grow slowly to cope with extended periods without food (Bradley et al., 2000, Hamer et al., 1997, Oka, 2011, Schultz and Klomp, 2000). Chicks fledge independent of their parents during the last week of April (Oka, 1989).

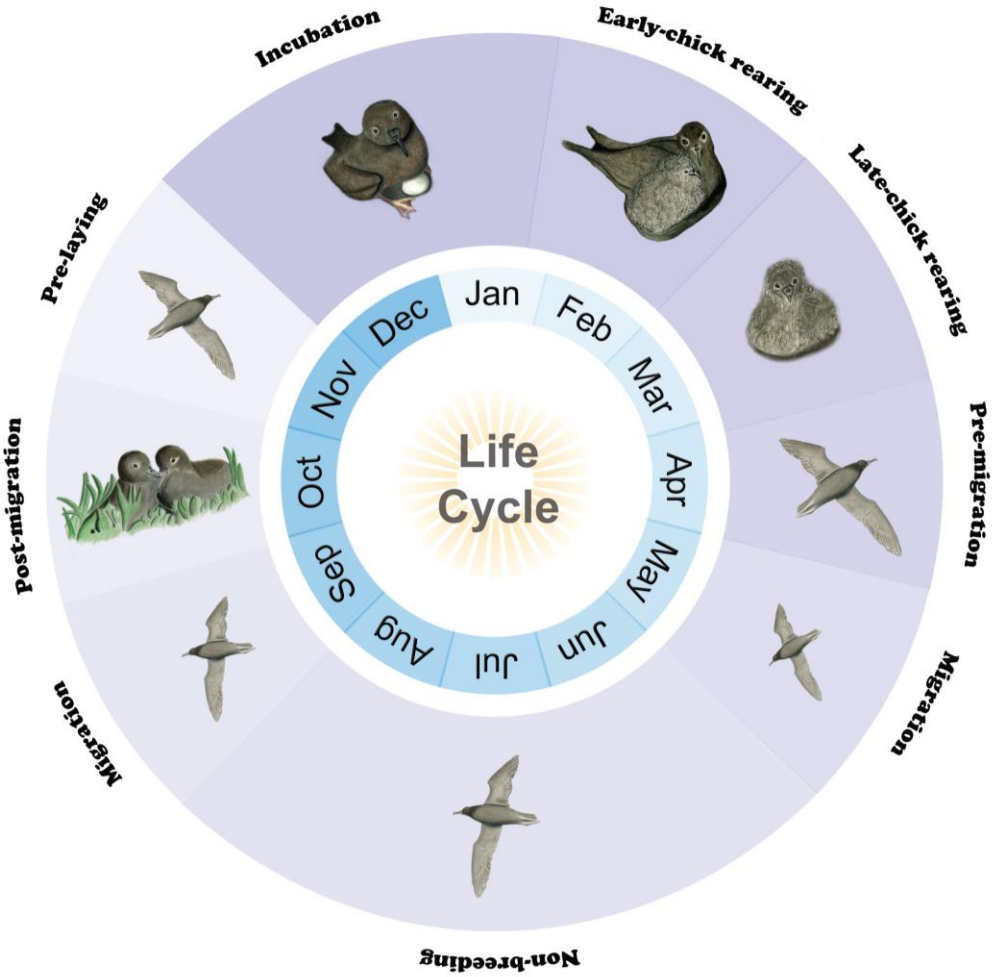

Figure 1.2. The annual life-cycle of the short-tailed shearwater. *Pre-laying* (October 25 - November 20), *Incubation* (November 20 - January 20), the *Early-chick rearing* stage (January 21 - February 28), and the *Late-chick rearing* stage (March 1 - April 8), *Pre-migration* (April - May), *Migration* (May), *the Non-breeding* stage (June - September), *Migration* (September - October), and *Post-migration* (October).

The oceanography of the regions utilised by short-tailed shearwaters

The Southern Ocean marine environment

The Antarctic Circumpolar Current (ACC) governs the Southern Oceans large-scale physical oceanography. The ACC is unique in that it is largely unobstructed by land, it circles the globe, and connects the Indian, Atlantic, and Pacific Oceans; flowing eastwards transporting nutrients and phytoplankton throughout the Southern Ocean basin (Orsi et al., 1995, Rintoul and Sokolov, 2001, Sokolov and Rintoul, 2009). Westerly winds are responsible for the movement of the ACC and the production of the Ekman current, which, promotes up-welling south of the ACC and down-welling to its north (Lenn and Chereskin, 2009, Roach et al., 2015, Trenberth et al., 1990). The fronts of the ACC are largely determined by topographical ridges, and at its most northern locality, extends within 200 km of southern Australia (Orsi et al., 1995). The ACC flow concentrates along the Southern Ocean Fronts, the sub-Tropical Front (STF), the sub-Antarctic Front (SAF), the Polar Front (PF) and the southern ACC front (SAACF) (Sokolov and Rintoul, 2009) (Figure 1.3). These frontal zones are coupled with high chlorophyll levels and enhanced productivity due to the convergence and upwelling of water masses bringing nutrients to the surface (Arrigo et al., 1998, Moore and Abbott, 2002). The Southern Ocean fronts mark the boundary between the water masses of the sub-Antarctic Zone (SAZ), Polar Frontal Zone (PFZ) and the Antarctic Zone (AZ), with discernible sea surface temperature (SST) and salinity gradients delineating the boundaries of each of these zones (Belkin and Gordon, 1996, Hamilton, 2006, Orsi et al., 1995).

Overall, the production of phytoplankton in the Southern Ocean is low and sparsely distributed, despite the high abundance of macro-nutrients (Arrigo et al., 2008, Moore and Abbott, 2000). The input sources of iron are limited and this restricts the growth and abundance of phytoplankton (Boyd et al., 2001, Coale et al., 2004, Moore et al., 2013, Petrou et al., 2016). The AZ is more productive compared to the other Southern Ocean zones due to higher levels of silicic acid, nitrate and iron (Zentara and Kamykowski, 1981), which promotes higher concentrations of chlorophyll *a* (Iida and Odate, 2014). Areas adjoining the Marginal Ice Zone (MIZ) in the AZ are productive due to iron run-off from the Antarctic landmass and seasonal ice melt, supporting a stable mixed layer and ice-edge algal blooms (Hoppe et al., 2017, Smetacek and Nicol, 2005). The Antarctic Divergence and the westward flowing Antarctic Current are also sites of enhanced productivity (Massom and Stammerjohn,

2010) and, dense aggregations of krill (Atkinson et al., 2004), marine mammals and seabirds (Brierley and Thomas, 2002), gather in regions where sea ice is maximal (Nicol et al., 2000). In contrast, the SAZ is characterised by high nitrate but low chlorophyll *a* quantities and shows little seasonal variability (Banse, 1996). Low sun angles, deep mixing of the water column and grazing by micro- and nano heterotrophs and limited micronutrients are believed to contribute to the low levels of chlorophyll *a* in this region (Boyd et al., 2000, Pearce et al., 2010, Safi et al., 2007). However, there is often heightened productivity in the waters surrounding sub-Antarctic islands due to iron run-off and increased nutrients where breeding colonies of marine predators occur (Boyd et al., 2000, Pollard et al., 2009, Smetacek and Nicol, 2005).

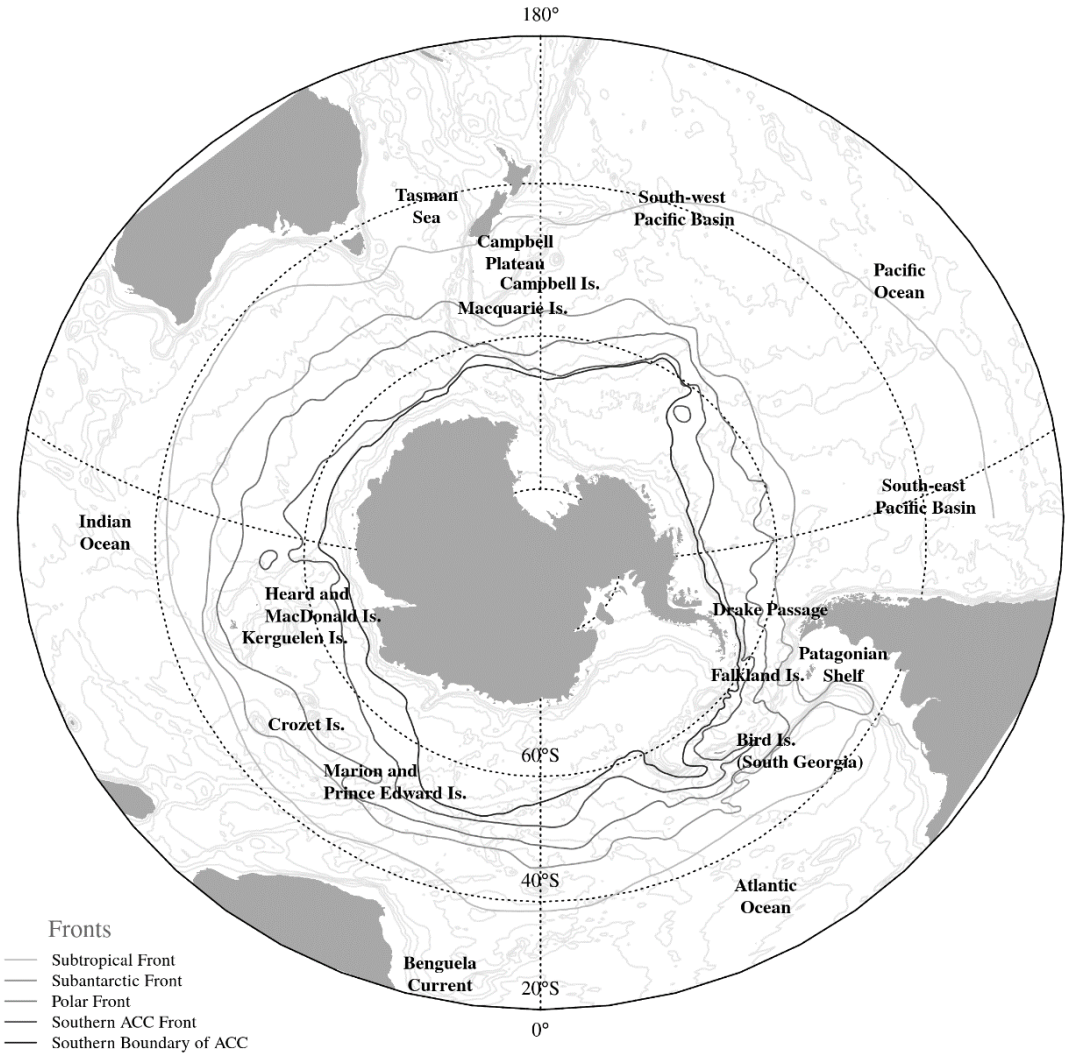

Figure 1.3. Circumpolar map of the Southern Ocean. The locations of the following fronts are shown: Sub-Tropical Front (STF), Sub-Antarctic Front (SAF), Polar Front (PF), Southern Antarctic Circumpolar Current (SACC) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC).

Seasonal primary production

The Antarctic is characterised by extreme light and temperature polarities between the winter and summer months. Subsequently peaks in primary production coincide with increased light availability, and when melting sea ice releases algae that activate algal blooms (Massom and Stammerjohn, 2010, Smith and Comiso, 2008). Phytoplankton and its spring blooms make up the base of the Southern Ocean marine system; its abundance is closely coupled with seasonal sea ice extent (Arrigo et al., 2008). Sea ice reaches its maximum extent in September to October and fully retreats by February to March (Knox, 2007). In conjunction, seasonal chlorophyll *a* and phytoplankton abundance follow the retreat of sea ice and ensuing daylight hours, reaching peak biomass by mid-January and decreasing after that point (Arrigo et al., 2008, Smith et al., 2000). This predictable pattern in seasonal production provides a signal to Southern Ocean organisms to commence reproduction (Doney et al., 2012). However, the magnitude of primary production varies spatially and temporally and this influences the abundance and growth of krill and its dependent predators (Constable et al., 2014, Fielding et al., 2014). Therefore, disruption of the onset of seasonal ocean productivity can have ecosystem-wide ramifications in the Southern Ocean (Moline et al., 2008).

Large-scale climate variability associated with the Southern Annular Mode

The seasonal atmosphere interactions that determine the retreat and advance of Antarctic sea ice are determined by the climate modes the Southern Annular Mode (SAM) and the El Niño –Southern Oscillation (ENSO) and its associated La Niña and El Niño phases (Stammerjohn et al., 2008b). There is co-variability with these modes, a positive ENSO phase coincides with a negative SAM phase, with the former linked to increases in global temperatures (Wang and Cai, 2013). The influence of these modes on sea ice extent anomalies is greatest during the Austral winter months, most likely because of increased SST (Marshall, 2003, Simpkins et al., 2012). However, the relationship between the two modes has weakened since the 1970s despite heightened ENSO activity; although ENSO is thought to have less influence on sea ice variability than the SAM (Simpkins et al., 2012).

The strength of the westerly winds that push the ACC, forcing upwelling which create nutrient rich eddies, are dominated by the seesaw of sea level pressure between the high and low latitudes of the Southern Ocean. The SAM provides a measure of the variability of sea

level pressure in the Southern Hemisphere, with a positive SAM event being associated with lower sea level pressure at high latitudes and higher sea level pressure at mid-latitudes (Thompson and Wallace, 2000). Southern Hemisphere surface temperature, sea ice and wind strength are strongly related to the SAM (Hall and Visbeck, 2002, Thompson and Solomon, 2002). The westerly wind belt has strengthened and shifted pole-wards due to the dominance of positive phases of the SAM in recent decades (Marshall et al., 2004, Thompson and Solomon, 2002), producing favourable primary productivity in high latitude areas at a cost to productivity in mid latitudes (Marshall, 2003). This positive trend is linked to ozone depletion, greenhouse gases and increasing global temperatures (Arblaster et al., 2011, Gillett and Thompson, 2003, Marshall et al., 2004, Wang and Cai, 2013). However, the contribution of natural internal climate circulation anomalies cannot be discounted (Fogt and Bromwich, 2006, Marshall et al., 2013).

The association between SST, sea ice extent and the SAM varies across the Southern Ocean (Simpkins et al., 2012, Stammerjohn et al., 2008b). Although the Southern Ocean is interconnected by the ACC, there are food-webs which are spatially distinct as a consequence of the interplay of regional oceanographic and climate mechanisms (Trathan et al., 2007). For example, a positive SAM event corresponds to warm northerly winds and a shortened sea ice season in the Antarctic Peninsula, Southern Bellingshausen Sea and the Weddell Sea (Lefebvre et al., 2004, Massom and Stammerjohn, 2010, Stammerjohn et al., 2008b); whereas the predominance of positive SAM phases is generating cool southerly winds in the Western Ross Sea, which are extending the duration of the sea ice season there. Nonetheless, relationships with the SAM, the ACC, and sea ice extent and its subsequent effect on the concentration of chlorophyll *a* anomalies have been established (Gille et al., 2016, Hall and Visbeck, 2002, Liau and Chao, 2017, Saba et al., 2014). Given the influence the SAM has on sea ice extent, surface temperatures, wind strength and primary productivity, it is a suitable proxy of seabird prey availability in the Southern Ocean.

The non-breeding stage of the short-tailed shearwater

Primary production in the Southern Ocean is highly seasonal and, in response, short-tailed shearwaters have adapted to this short-term availability of prey by migrating to the productive waters of the North Pacific Ocean (Figure 1.4) during the Austral winter (Carey et al., 2014, Ito, 2002). The birds travel over 15,000 km to reach the North Pacific foraging

region, travelling ~840 km per day using the prevailing winds (Carey et al., 2014, Ito, 2002, Nicholls et al., 1998, Yamamoto et al., 2015). At present there is little known about the foraging strategies of short-tailed shearwaters during the non-breeding stage, but at-sea observations and tracking studies indicate that the foraging behaviour of these birds is influenced by SST (Yamamoto et al., 2015) and the availability of krill (Hunt et al., 2014, Nishizawa et al., 2017).

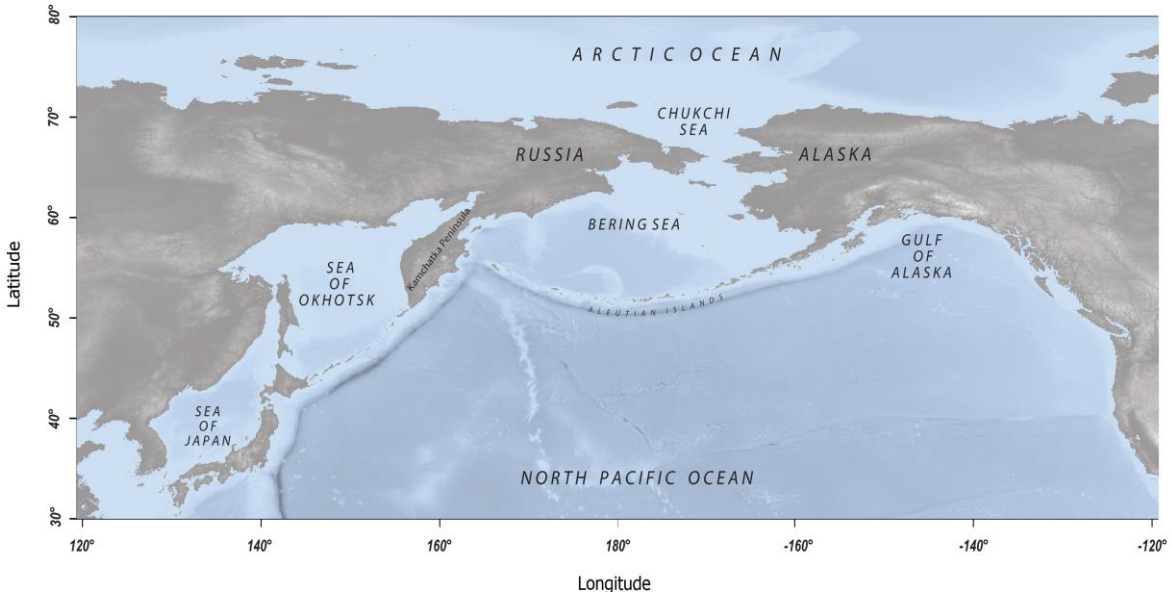

Figure 1.4. The seas used by short-tailed shearwaters during the non-breeding season. The Sea of Japan, the Sea of Okhotsk, the North Pacific Ocean, the Bering Sea, the Chukchi Sea and the Gulf of Alaska.

Oceanography of the non-breeding foraging regions visited by short-tailed shearwaters

The Bering Sea

The Bering Sea is juxtaposed between the North Pacific and Arctic ecosystems and is geologically segmented by the shelf break (> 200 m), which splits the continental shelf from the ocean basin (maximum depth 3500 m) (Springer et al., 1996, Stauffer et al., 2014). The Bering Sea is enclosed by the Aleutian Islands at its southern extent and the Bering Strait connects the Pacific and Arctic Oceans at the most northern range of this sea, and it is bounded by the Russian Coastline to the west and the Alaskan coastline to the east (Figure 1.5). The eastern Bering Sea shelf is > 500 km wide and extends northwards along the Alaska Peninsula to the Bering Strait (Stabeno et al., 2012b). Water enters the Bering Sea through several passes in the Aleutian Island chain circulating through the Bering Sea in an anti-

clockwise direction via the Aleutian North Slope Current (ANSC) which travels eastwards along the Aleutian Islands until it meets the northwest flowing Bering Slope Current (BSC) (Aydin and Mueter, 2007, Stabeno et al., 1999). Water is then transported through the Kamchatka Straight via the south west flowing Kamchatka Current (KC) (Aydin and Mueter, 2007, Stabeno et al., 1999). In addition to these currents, water flows northwards through the Bering Strait via the Alaska Coastal Current (ACC) to the east and from the west via the Anadyr Current (AC). Sea ice begins forming by mid-December, reaching its maximum extent in February to March, but the Bering Sea is usually free of sea ice during summer and most of autumn (Stabeno et al., 2012a). In cold years sea ice extends to the Alaskan Peninsula but stays north of 58°N in warm years.

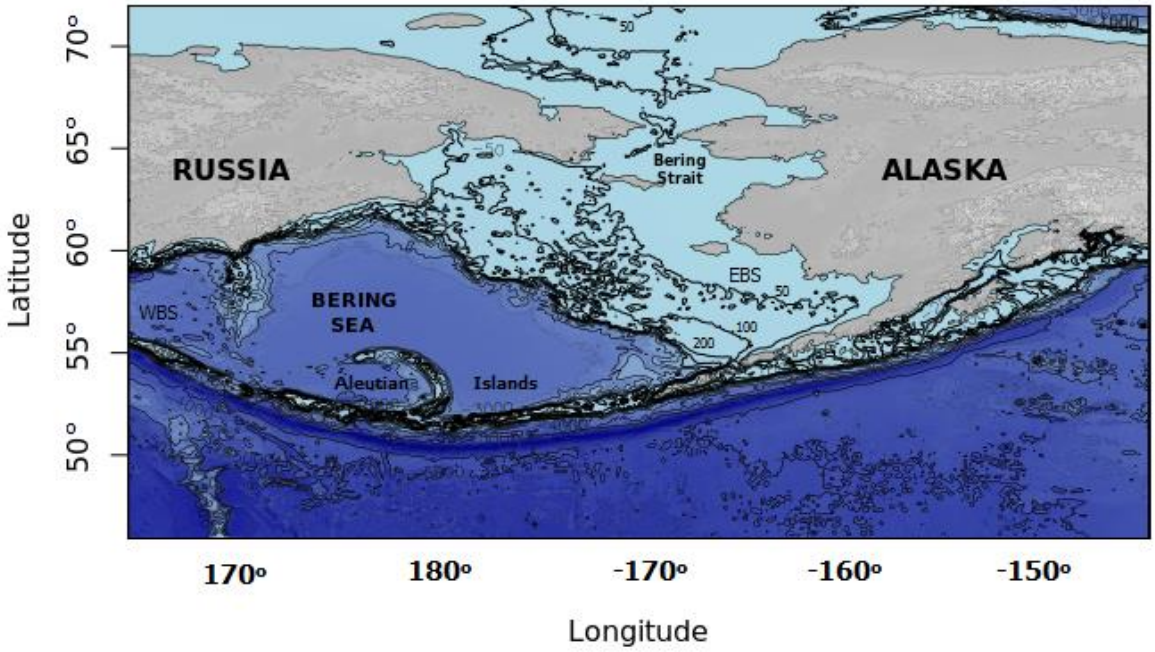

Figure 1.5. The biogeographic regions of the Bering Sea. The Western Bering Sea (WBS) and eastern Bering Sea (EBS) and bathymetric contours are depicted by the black lines. Light blue denotes shallow shelf areas (0 - 200 m) and dark blue signifies deep ocean waters < 5000 m.

Chukchi Sea

The Chukchi Sea is a marginal Arctic Sea transition zone between the Pacific and Arctic Oceans (Figure 1.6) (Ershova et al., 2015). It is characterised by a low shelf region (~80 m) (Carmack and Wassmann, 2006, Grebmeier et al., 2006a, Hunt et al., 2013) with the southern boundary at 66°N extending to the continental shelf of the Arctic Ocean (Hunt et al., 2013,

Woodgate et al., 2005). Water flows from the Pacific Ocean through the Bering Strait into the Chukchi Sea. The Chukchi Sea is completely ice-covered during winter, but is free of ice June – mid October (Gall et al., 2013). Low sea temperatures during winter through early spring in the Northern Bering and Chukchi Seas limit zooplankton growth and reproduction, with most nutrients sinking to the sea floor, which supports benthic production during this period (for a review see Grebmeier et al., 2006a). However, high spring blooms occur as marginal sea ice retreats.

Like the near shore regions of the northern Bering Sea, the Chukchi Sea is typically low in nutrients, but the incursion of nutrient rich Pacific Ocean waters enhances productivity (Grebmeier et al., 2006a). The shelf boundary areas are also influenced considerably in summer by Pacific Ocean water through the injection of nutrients, phytoplankton and zooplankton (Grebmeier et al., 2006a, Hunt et al., 2013). Three water masses are also responsible for the flow of nutrients through the Chukchi Sea. The Anadyr Water (AW), which originates from the continental slope of the Bering Sea, is cool and nutrient rich, and flows northwards to the west (Grebmeier et al., 2006a and references within). The fresher warmer Alaska Coastal Water (ACW) is moved north from the Bering Sea Shelf along the coastal boundaries by the Alaska Coastal Current (ACC). Located between the AW and the ACC, Bering Shelf Water (BSW) mixes with AW forming the Bering Shelf Anadyr Water (BSAW), creating a strong frontal system during the open water season (Ahlnäs and Garrison, 1984, Grebmeier et al., 2006a and references within).

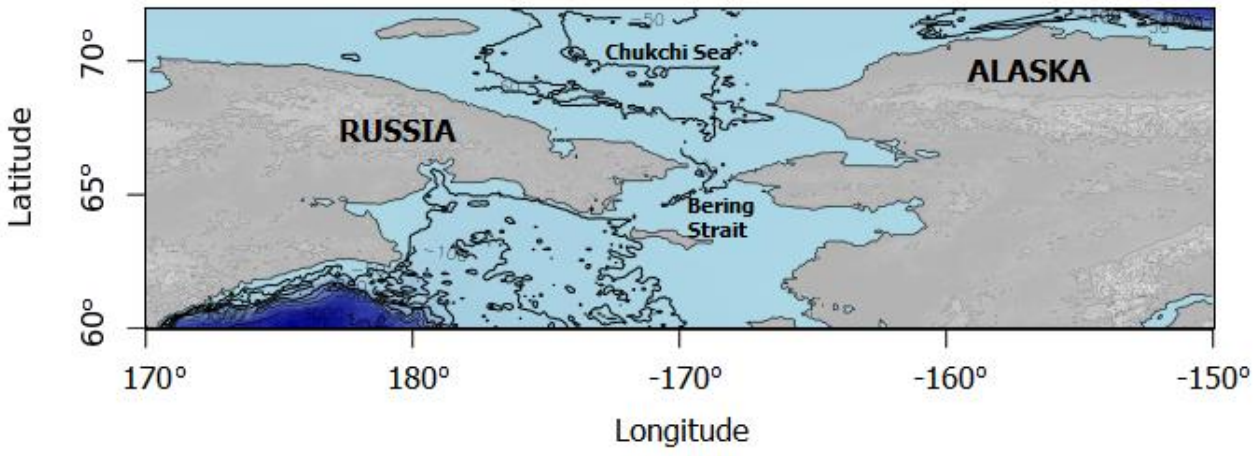

Figure 1.6. The Chukchi Sea. Bathymetric contour lines are indicated by the black lines.

Sea of Okhotsk and the Sea of Japan

The Sea of Okhotsk is bounded by the Far Eastern Siberian coast to the west, the Kamchatka Peninsula and Kuril Strait to the east and it borders the north eastern coastline of Japan to the south (Figure 1.7). The Okhotsk Sea gyre transports water in a counter clockwise direction (Tanabe et al., 2017). Water enters the Sea of Okhotsk from both the North West Pacific via the Kuril Straits and from the Sea of Japan via the Soya and Mamiya Straits (Simizu and Ohshima, 2006). The main bathymetric features of the sea include a continental shelf located in the northwest with depths not exceeding 200 m, a central basin (1000 -1600 m deep) and the Kuril Basin is located at the southern extent of the sea (maximum depth 3000 m) (Preller and Hogan, 1998, Simizu and Ohshima, 2006). During November sea ice forms along the northwest coast, reaching its maximum extent by February to March (Simizu and Ohshima, 2006). Increasing spring temperatures result in the melting of most of the sea ice by the end of May (Simizu and Ohshima, 2006, Tanabe et al., 2017).

The Sea of Japan is also a semi-enclosed sea but, unlike the Sea of Okhotsk, it is characterised by having a deep ocean basin (~1350 m), and lacking a continental shelf, although the waters surrounding the Soya and Mamiya Straits are shallow (~150 m) (Gamo and Horibe, 1983 and references within). Unlike the Sea of Okhotsk, sea ice does not form during winter.

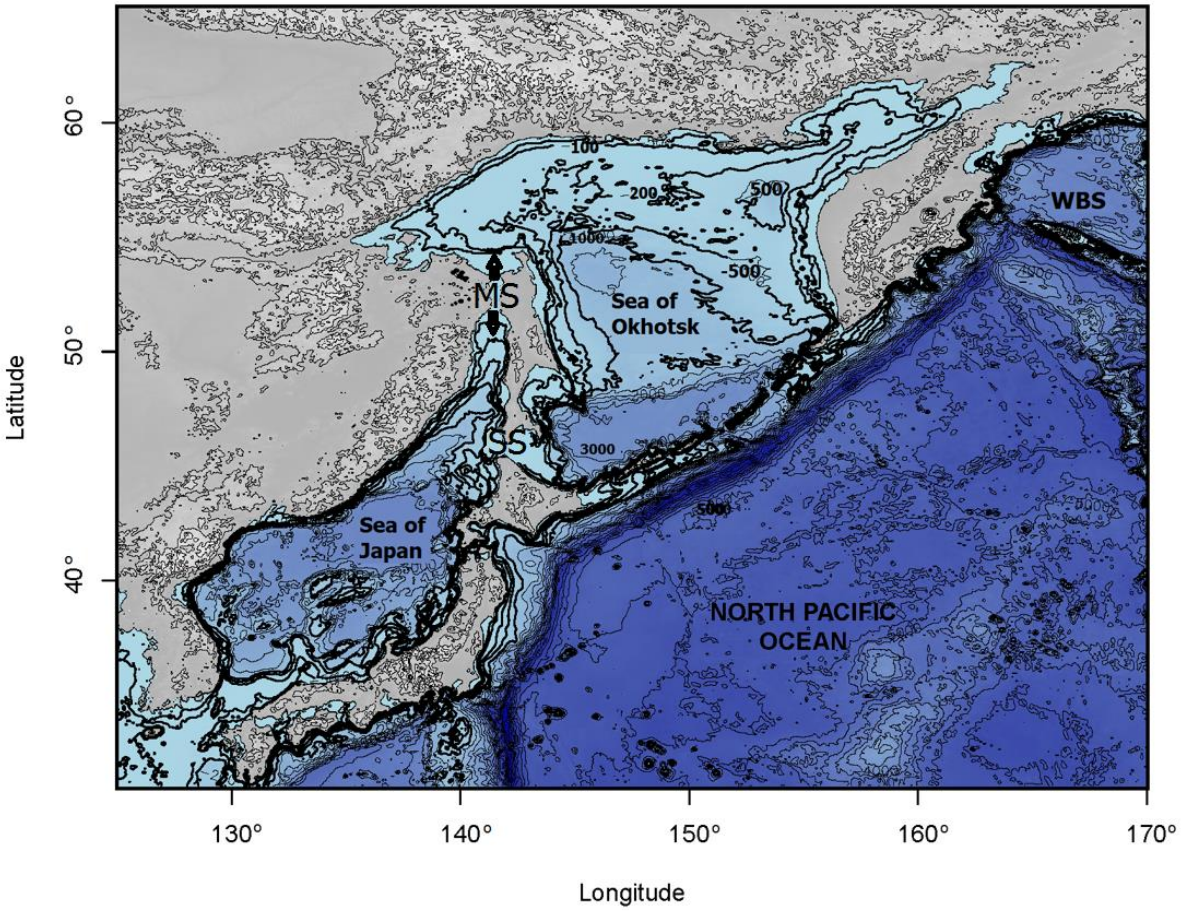

Figure 1.7. The biogeographic regions of the Sea of Japan and the Sea of Okhotsk. Bathymetric contours are depicted by the black lines. Light blue denotes shallow shelf areas (0 - 200 m) and dark blue signifies deep ocean waters < 5000 m. SS = Soya strait, MS = Mamiya Strait.

Climate trends in the North Pacific

Climate change has the potential to drastically affect the North Pacific food web as increasingly warm temperatures are changing sea ice dynamics (Johannessen et al., 2004, Markus et al., 2009, Wood et al., 2015). Shifts in the environment and community dynamics of the North Pacific are closely related to the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO) (Overland and Stabeno, 2004, Stabeno and Overland, 2001, Thompson and Wallace, 1998). The PDO is the monthly index of climate >20°N of the North Pacific Basin. Positive values correspond to anomalously warm SST while negative values indicate anomalously cold conditions (Mantua and Hare, 2002). The AO ranges between positive and negative modes, much like the SAM, and indicates the exchange of atmospheric wind component (centred at 45°N) between the Arctic and mid-latitudes in the Northern

Hemisphere (Thompson and Wallace, 1998). This index has also been trending towards positive (anomalous low pressure over the Arctic) and this results in thinner sea ice which is more prone to melt in early Spring (Rigor et al., 2002). During the winter of 2015 sea ice in the Sea of Okhotsk was at its lowest extent since 1979 (Paik et al., 2017). While there has been rapid sea ice decline in the past three decades in the Chukchi Sea and Sea of Okhotsk, the Bering Sea has had greater fluxes in sea ice extent and has even undergone periods of extended winter sea ice cover (Frey et al., 2015, Paik et al., 2017). Such linkages between ocean productivity and climate affect the distribution (Kuletz et al., 2015, Kuletz et al., 2014), breeding success and population stability of seabirds in the region (Kitaysky and Golubova, 2000, Kitaysky et al., 2006, Springer et al., 2007, Watanuki and Ito, 2012). These changes in sea ice extent and duration, currents and the location of fronts have the potential to cause long-term changes to the food base which marine predators rely upon and this is cause for concern (Carmack and Wassmann, 2006, Hunt et al., 2013, Sigler et al., 2011).

Study site

Wedge Island – southeast Tasmania

In this thesis, to examine the responses of the short-tailed shearwater to a changing climate, research was undertaken at Wedge Island, 43°08'S, 147°40'E in southeast Tasmania, Australia (Figure 1.8). Wedge Island is at the southern extent of the short-tailed shearwater's breeding range, it supports a colony of ~25,000 breeding pairs of short-tailed shearwaters, and a small colony of ~500 breeding pairs of little penguins (*Eudyptula minor*) (Vertigan, 2010). The island is 42 hectares in size, 1.3 km long and is dominated by *Poa poiformis, C. rossii* and *Rhagodia candolleana* (Brothers et al., 2001). Human presence is minimal as slippery boulders deter most boat enthusiasts from landing. Currently there are no introduced mammalian predators on Wedge Island. Feral cats were removed in 2003 and sheep grazing ceased in 1986, although native water rats (*Hydromys chrysogaster)* and forest ravens (*Corvus tasmanicus)* are present. Both of these species have been observed to prey on short-tailed shearwater chicks (N.Bool pers. Obs). Dead preyed upon adult shearwaters are frequently encountered on the island; resident swamp harriers (*Circus approximans)* and brown falcons *(Falco berigora)* may kill adults, although such an event has not been witnessed, it could occur. However, predation by land-based animals on short-tailed

shearwaters has not been quantified at this colony and. as such, what influence these have on the population is unknown.

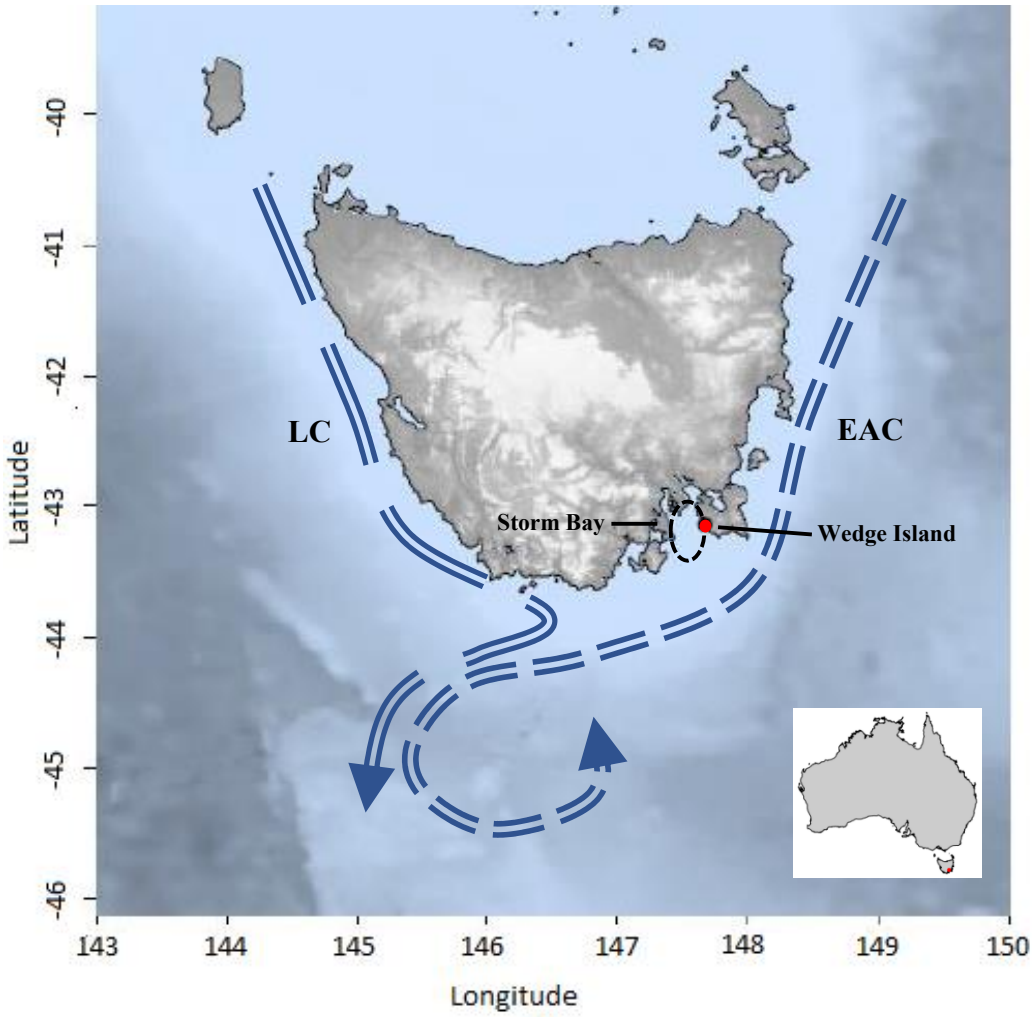

Figure 1.8. The location of Wedge Island and Storm Bay, Tasmania, Australia. The approximate flow of the East Australian Current (EAC) and Leeuwin Currents (LC) (dashed lines) during the austral summer (adapted from Cresswell (2000)).

Oceanography of the waters surrounding Wedge Island

Wedge Island is situated ~1 km off the Tasman Peninsula within the shallow waters of Storm Bay (30 - 85 m), which is ~500 km^2 in area (Clementson et al., 1989). The continental shelf extends along the 19 km perimeter of the bay, where water depth drops to ~2000 m beyond the shelf region (Reid and Hindell, 2000). The primary production of Storm Bay is influenced by the Leeuwin Current as it brings waters (~12°C) south from the north-west of Tasmania during winter, and the East Australian Current (EAC) that transports warm, saline waters from the north-east during summer (~16°C) (Cresswell, 2000, Ridgway and Condie, 2004). The EAC is a pole-ward flowing boundary current that separates from the east-Australian mainland at 32.5°S (Ridgway, 2007). The flow of the EAC has extended further south in recent years, leading to incursions of nutrient poor saline water into Southern Tasmania, which is negatively influencing the production of phytoplankton (Buchanan et al., 2014). To the south of Storm Bay, the STF signifies the boundary between the warm, salty water of the Tasman Sea and the comparatively cooler nutrient rich sub-Antarctic waters (Hamilton, 2006, Harris et al., 1992). The positions of these fronts are influenced by wind, causing them to move north and southwards seasonally (Sikes et al., 2009). Sub-Antarctic waters move into southeast Tasmania during summer when the EAC and LC currents are weakened, boosting nutrient flow which supports phytoplankton growth and the abundance of zooplankton and fish (Buchanan et al., 2014, Harris et al., 1987). Short-tailed shearwaters depend on this predictable upwelling of nutrient rich waters to raise their chicks.

Thesis aims

The environments in which seabirds live are changing; the degree to which they can adapt will vary dependent on their life-history traits, dispersal capabilities and dietary breadth. This thesis investigates the capacity of short-tailed shearwaters to adapt to a rapidly changing environment. The short-tailed shearwater is presented as a suitable model species as it has several specialised life-history traits, such as long generation times, low fecundity, and bi-modal foraging during chick rearing. The short-tailed shearwaters foraging habitat is divided between the North Pacific Ocean during the non-breeding stage and the Southern Ocean whilst breeding. These regions are particularly sensitive to climate perturbations and with global temperatures currently warming the dynamics of these marine environments may change faster than this long-lived species can adapt. Therefore, to better understand how the

short-tailed shearwater responds to climate enforced changes in the distribution of its prey and how this affects the species' overall population viability, I specifically aimed to 1) examine the non-breeding movements of adults and assess the within-season prevalence of foraging site fidelity; 2) determine the influence of climate on trophic position during the breeding season; and 3) evaluate how climate variability during the breeding season influences foraging distribution, breeding participation and success, and the mass of fledglings.

Thesis structure

This thesis comprises three separate chapters on the foraging ecology of short-tailed shearwaters during the breeding and non-breeding stages. These chapters have been written with the intent of submitting them to peer reviewed journals for publication. There is consequently some duplication between chapters.

Chapter 2: explores the foraging strategies of short-tailed shearwaters during the non-breeding stage and identifies two core staging areas and highlights how the environment is changing within them.

Chapter 3: investigates whether the stable isotope values of adult birds are influenced by baseline variability in the foraging regions and whether the trophic position of short-tailed shearwaters is variable under fluctuating environmental conditions during the breeding season.

Chapter 4: measures of ocean productivity are used to explain 1) foraging behaviour during the breeding season and 2) inter-annual variability in the number of birds engaging in breeding activities and breeding success.

Chapter 5: presents a synthesis of the main findings of this PhD thesis.

CHAPTER 2 HIERARCHICAL FORAGING STRATEGIES OF SHORT-TAILED SHEARWATERS DURING THE NON-BREEDING SEASON

Abstract

Foraging specialisations are common in animal populations as these can increase the rate at which individuals acquire food. However, foraging plasticity may become increasingly important in variable or changing environments. To better understand the capacity of migratory seabirds to adapt to changing environmental conditions, we set out to determine how plastic the feeding behaviours were of 60 short-tailed shearwaters (*Ardenna tenuirostris*) during the non-breeding season. The birds showed individual foraging site selection, predominantly using one of two non-breeding staging areas, the Sea of Okhotsk/North Pacific Ocean (Western group), and the southeast Bering Sea/North Pacific (Eastern group). Eight birds, which were tracked for two consecutive years returned to the same core winter staging areas, but the time they spent in these regions, varied among years. Overall, 50% of the birds left their core area and moved into the Chukchi Sea toward the end of the non-breeding stage suggesting that the birds have a flexible within-season foraging strategy. We found that seasonal patterns in chlorophyll *a* concentrations broadly mirrored the timing of the movement of birds out of their core foraging regions. This move also likely coincided with the availability of large bodied krill in the secondary foraging region. This hierarchical strategy, where individuals return to familiar areas but disperse if environmental conditions decline, would allow short-tailed shearwaters to buffer some of the effects that climate variability would have on the distribution and abundance of their prey. Such flexibility could be important if short-tailed shearwaters are to be resilient to climate induced environmental change.

Introduction

Knowing where individuals find their food and how they adapt their foraging strategies in response to changes in its distribution and abundance is an important component of animal ecological studies. In the marine environment, resources fluctuate within and among seasons, so predators must learn to identify where resources can be predictably found (Petrou et al., 2016, Yoo et al., 2008). Physical features such as fronts, continental shelves and slope areas, and sites of up-welling are particularly important as they can provide predictable dense aggregations of prey for marine predators in otherwise ephemeral environments (Bost et al., 2009, Lea et al., 2006, Lee et al., 2017, Weimerskirch, 2007). Accordingly, marine predators

tend to show fidelity to these features (Nel et al., 2001, Patrick and Weimerskirch, 2014, Queiroz et al., 2012). When individuals repeatedly return to the same foraging sites they gain experience in how to find prey in that habitat, increasing foraging efficiency (Phillips et al., 2017, Piper, 2011). Consequently, foraging site fidelity can be maintained over a number of days to months and these sites may be revisited over many years (Arthur et al., 2015, Auge et al., 2014, Bradshaw et al., 2004, Samarra et al., 2017).

The sites to which individuals show fidelity during the non-breeding stage is important, as the amount of energy accrued can affect other stages of the annual cycle, influencing both short-term survival and subsequent reproductive output (Abrahms et al., 2018, Fayet et al., 2016b, Harrison et al., 2011, Shoji et al., 2015). For marine predators that migrate after breeding to exploit remote seasonally available resources, the costs of migration must be outweighed by energy gained in the non-breeding habitat (Cox, 1985, Lea et al., 2015, Ramenofsky and Wingfield, 2007). Particularly as the availability of resources at the migration terminus is likely to influence short-term fitness because individuals need to quickly recover lost reserves (Baduini et al., 2001b, Baker et al., 2004, Lennox et al., 2016). Therefore, if individuals return to sites which they are familiar with, and where resources can be predictably located, could both reduce searching time and increase the rate at which prey is encountered. However, if broad-scale environmental conditions change unidirectionally then high levels of site fidelity could prove to be disadvantageous (Bolnick et al., 2003, Forcada et al., 2008, Travis et al., 2013). Under such conditions, a hierarchical strategy that incorporates site fidelity when resources are predictable and the dispersal of individuals when conditions are poor, may increase prey encounters within a season (Switzer, 1993).

The migratory short-tailed shearwater (*Ardenna tenuirostris*) is a long-lived seabird that leaves its breeding colonies in southern Australia and spends the non-breeding stage, May to October, in the North Pacific Ocean (Skira, 1991). During this time short-tailed shearwaters use waters of the Sea of Japan, the Bering Sea, the Gulf of Alaska and the Chukchi Sea (Carey et al., 2014, Yamamoto et al., 2015) where individuals are thought to use the same foraging areas for extended periods (Baduini et al., 2006, Hunt et al., 2002). The existence of a number of non-breeding staging areas (in this case with respect to foraging site) within the population may allow short-tailed shearwaters to maximise foraging success both during and among years. The non-breeding regions in the Northern Hemisphere that are used by short-

tailed shearwaters have been undergoing considerable environmental change in recent decades (Brown et al., 2011, Grebmeier et al., 2006b, Ogi et al., 2015, Overland et al., 2008). This is causing shifts in sea ice dynamics, which influences the location and timing of spring blooms, water column temperature and stratification (Brown et al., 2011, Duffy-Anderson et al., 2017, Hunt et al., 2011). Ultimately this regulates the distribution and abundance of the resources that short-tailed shearwaters and other marine predators depend on (Bluhm and Gradinger, 2008, Gall et al., 2017, Grebmeier et al., 2006b, Trites and Donnelly, 2003). Therefore, we aimed to study the non-breeding foraging behaviour of short-tailed shearwaters to determine: 1) whether individuals diverge in their selection of primary staging sites; 2) if individuals maintain fidelity to their primary staging areas between years; 3) do the individuals using different staging areas have equivalent levels of foraging activity (time spent in the water); 4) the environmental conditions underpinning the core foraging regions; and 5) whether environmental conditions are changing over time and what the implications are for the maintenance of specific strategies.

Methods

Ethics statement

All animal handling and instrumentation were carried-out under Research Permits (DPIPWE: FA10212, FA13009, FA14063, FA15083, FA16077) and University of Tasmania Animal Ethics Committee permits (A11338, A128942, A15572).

Study site and species

This study was conducted at Wedge Island, southeast Tasmania, Australia (43° 07’ S, 147° 40’ E), from 2012 to 2015. The short-tailed shearwater is a medium sized Procellariiforme seabird that breeds in southern Australia during the Austral summer (October - April) and migrates to the Northern Hemisphere for the non-breeding season (April - October) (Marshall and Serventy, 1956).

Global location sensors (GLS)

Shearwater movements and distribution during the non-breeding season were estimated with global location sensing (GLS) devices. The GLS devices were deployed from 2011 to 2015.

GLS devices were deployed on average for 11 months (range 7 – 52 months). Devices were deployed as part of a larger study concerning breeding movements. Hence, the devices used in this study were deployed throughout the breeding season from October to April. For details of logger deployments and retrievals by month and year see Appendix 2.1. Three types of GLS devices were used over the course of the study: (1) MK19 GLS tags (British Antarctic Survey, Cambridge, UK; 16x14x6 mm, 2.5 g) were deployed during the 2011 breeding season; (2) MK3005 GLS tags (Biotrack Ltd., Wareham, UK; 2.5 g) were deployed in 2012 and 2013; and (3) Intigeo ®C250 GLS devices (Migrate Tech Ltd, Cambridge, UK; 18X15X6 mm, 3 g) were deployed in 2014 and 2015 (Table 2.1). All the tags collected ambient light, activity (wet/dry events) and sea surface temperature data (SST; -0.125°C resolution). The GLS tags sampled ambient light every minute and recorded the maximum light level every five minutes, which was used to estimate the birds' location (Hill, 1994).Water temperature ± 0.5°C was recorded when the device was continuously wet for 20 minutes. Minimum, maximum and mean temperatures were sampled every four hours for the C250 tags, allowing the data to be compared to remotely sensed SST. The MK19 and MK3005 tags provided temperature data when devices were submerged for 25 minutes, but when the sensor was dry for six seconds or longer they stopped recording. All loggers used in this study recorded activity data, which was used to infer foraging behaviour, either foraging or resting on the surface (wet) or flying continuously for over 25 minutes (dry). The MK19 and MK3005 tags recorded activity data (number of seconds wet/dry) on state change (within three seconds), if the state persisted for longer than six seconds ranging from 0 (always dry) to 200 (always wet). The C250 tags recorded the state (either wet or dry) and the number of seconds since a change in state, providing the amount of time the bird was either in flight or in or on the water.

Tags were attached to the tarsus after Cleeland et al. (2014). The maximum weight of the tag and attachment was 4.5 g, < 1% of the mean mass (597.1 ± 57.3 g, n = 421) of the birds. Tags were calibrated at the deployment site by placing them under the open sky for 2 to 7 days prior to deployment to provide light recordings at a known location allowing for accurate estimation of sun elevation (Lisovski et al., 2012). A subset of non-tagged birds (n = 74) were weighed using a 1 kg (± 5 g) Salter spring balance (Super Samson models, Salter Australia Pty Ltd, Melbourne, Australia) and compared with those of tagged birds to check for device effects at the end of the return migration in October of each year. A total of 141 GLS tags

were deployed on adults during the breeding season (Table 2.1) and 93 GLS tags were retrieved during subsequent breeding seasons. All birds were recaptured at the colony, either in their burrows or on the surface near their burrows, except for one individual which was found dead on a beach in South Australia in 2013 (post-migration, cause of death unknown). Fifteen birds were re-captured 18 to 52 months after deployment. Of these, tags were missing from 4 birds and 2 tags had failed after deployment and a further tag contained corrupted data, resulting in data from 8 birds for 2 seasons. Overall, 5 loggers failed to collect any data (due to tag failure) and a subset of tags; 2 MK19 devices, 17 Biotrack Ltd, and 5 Migrate Tech Ltd devices failed 1 week to 3 months and 1 to 12 months after deployment respectively. Further to this, 6 recovered devices contained corrupted data and could not be used in analysis. Overall, a total of 60 devices provided data that were used in analyses. Due to the small sample size among years, data were pooled. Inter-annual differences were only investigated for the 8 birds that were tracked for two consecutive non-breeding stages.

Table 2.1. The year, the model, and the number of GLS devices deployed on and retrieved from short-tailed shearwaters at Wedge Island.

Year	Model	GLS deployed[a]	GLS recovered	Tracks included in analyses[b,c]	Activity data included in analyses[d]
2012	MK19	15	10	8	0
2013	MK3005	30	13	10*	4
2014	MK3005	32	27	7**	5
2015	MK3005 & C250	64	38	39	38
2016	C250	NA	5	4***	0
Total	**-**	**141**	**93**	**68**	**47**

a) Excluding birds tracked only for the breeding season.

b) Some tags failed during deployment and consequently did not provide data for the entire non-breeding stage. Data was only included if it were available for ~80% of the non-breeding stage. Resulting in 60 birds being included in analyses.

c) Includes data from 8 individuals that were tracked for 2 consecutive non-breeding stages.

d) The tags used in this study had limited capacity to store activity data (~ 7 months). In the instances where the logger had been deployed during the breeding season and/or for multiple years, the tag ceased recording activity data prior to the end of the non-breeding stage. Individual activity data were only included if it were available for ~80% of the non-breeding stage.

* Includes data from 3 devices retrieved in 2013 that were deployed during 2012 (providing consecutive non-breeding stage data).

** Includes data of a device retrieved in 2014 that was deployed during 2013 (providing consecutive non-breeding stage data).

*** Data from 5 devices retrieved in 2016 that were deployed in 2015 (providing consecutive non-breeding stage data).

Location processing

Daily positions were estimated from the raw light and sea surface temperature (SST) values recorded by the GLS devices in the R package `SGAT` (Sumner et al., 2009, Wotherspoon et al., 2013). This package uses the Threshold method (Hill, 1994), where location estimates are computed using the solar zenith angle calculated during the calibration period. Because the tags deployed on these birds were attached to their leg the sensor can sometimes be shaded by the bird when it is in flight or when it is sitting on the surface at the colony. Shading can considerably affect the estimation of latitude positions. Therefore, where shading of the tag's sensor prevented accurate estimation of the twilight curve, individual twilights were manually adjusted to match the overall trend in the light level prior to twilight, based on the set light threshold identified during the pre-processing stage. In addition, sometimes when birds sit on the surface at the colony or when nesting, wet/and or muddy and sufficiently salty feathers can result in false SST readings. These readings are typically anomalously higher than the median SST temperature, so this data was identified and removed using the SSTfilter and selectData functions in `SGAT`.

`SGAT` is based on a Bayesian framework that uses Markov Chain Monte Carlo (MCMC) to estimate the posterior distribution of locations (Sumner et al., 2009). Each birds' locations were estimated (and 95% CI) using a set of priors that include: 1) a spatial probability mask, to exclude locations on land, 2) a movement model where the average speed of travel between successive locations was assumed to be Gamma distributed, the probability of distribution of speeds is estimated using the mean time intervals between twilights (in hours), limiting the distance between locations, and, 3) to improve accuracy of location data, SST was used to constrain the location estimation. The final estimated track was calculated using a Metropolis algorithm to burn in 12 000 iterations. The posterior distribution of the filtered mean temperature data recorded by the device was compared to remote satellite derived SST data, obtained from the Earth System Research Laboratory http://www.esrl.noaa.gov/psd/repository/entry/show?entryid=12159560-ab82-48a1-b3e4-88ace20475cd) and, 4) to account for twilight errors associated with tag shading, a log-normal probability distribution was applied to twilights, providing more accurate location estimation (Wotherspoon et al., 2013).

Spatial analysis of foraging data

To categorise the Austral winter foraging distribution of the shearwaters, we considered the migration phase to have commenced when a bird moved north of 40°S, while the end of the northern migration was taken to be when a bird arrived at 40°N. From this, the total time spent in their non-breeding foraging areas, the highest latitude reached and the migration time (days) for each bird was determined. Examination of the location estimates in this study showed that birds were distributed between 40° - 80°N and 125°E - 135°W during the non-breeding season. To identify the areas of core use of each individual, we divided this region into 20° latitude by 10° longitude grid cells. Using the complete set of daily posterior location estimates produced by `SGAT` the proportion of time individual birds spent in each grid cell (calculated as a proportion of the total time spent between 40° - 80°N and 125° - 135°W) was determined.

Hierarchical cluster analysis using Ward's minimum variance method based on Euclidean distances (`hclust`, R Development Team) was used to identify groups of birds with the same patterns of spatial use of grid cells. Only cells that were used by more than three individuals were included in analyses to provide an indication of general usage of cells. Individuals were assigned to a group based on visual inspection of the resultant dendrogram. Using the daily location estimates of the individuals, both the core and home range estimates were calculated for each cluster group using the `adehabitatHR` package (Calenge, 2006). The 50% Kernel Utilisation Distribution (KUD) represented the core foraging area and 95% KUD was considered the home range (Wood et al.2000). The time individuals spent within their core foraging areas was calculated as a proportion of the total time they spent within the non-breeding region (> 40°N).

Activity data

Short-tailed shearwaters are known to forage during periods of darkness (Berlincourt et al., 2015). However, the birds in this study spent significantly more time on the water's surface during periods of darkness (t = -19.477, df = 17955, $p < 0.0001$), which was most likely associated with time spent resting due to limited visibility (Phalan et al., 2007, Shaffer et al., 2009, Wilson et al., 2009). Consequently, we excluded night activity data, as it was not possible to differentiate between periods of rafting or foraging. By combining the estimated

sunrise and sunset times with the location data to determine day length, we calculated the daily period spent on the water during daylight. To compare diurnal at-sea activity (time spent in or on the water, *pwe*t), the proportion of the daily total wet time was calculated for each bird and the data over-laid with the corresponding location estimates, to determine the *pwet* for each foraging region. This provided an index of at-sea foraging activity, which was used to compare the *pwet* among the groups. Although it is likely that a proportion of the time spent on the water's surface during daylight hours would be associated with resting rather than foraging, the amount of time a logger is wet is considered to provide an acceptable indication of seabird foraging activity (Catry et al., 2009, Krietsch et al., 2017).

Environmental data

To examine long-term environmental trends between the core areas used by the groups of birds, we characterised the environmental characteristics of each core foraging area using; chlorophyll *a* concentration (Chl *a*) (2003 - 2016), sea surface temperature (SST °C) (1983 - 2016), sea surface height (SSH) (1993 - 2016) and sea surface height anomaly (SSHa) (1993 - 2016). Data were obtained from the Australian Antarctic Data Centre and extracted using the `raadtools` package (Sumner, 2017) in R. The mean yearly value for each variable was calculated from daily values for each month that short-tailed shearwaters occupy the North Pacific (May to October).

Statistical analyses

We used a Two-Sample t-Test to compare body masses of birds returning from the Northern Hemisphere that were fitted with a GLS device to control birds. One-way ANOVAs were used to compare foraging parameters between cluster groups: i) whether the mean time spent in the core regions varied; ii) differences in the time taken to migrate to the North Pacific; and iii) the most northerly location reached. All dependent variables were log transformed when necessary if data deviated from a normal distribution and significance levels were set at $p < 0.05$. To assess whether the proportion of the day spent in the water (*pwet*) by individuals within their core foraging regions varied between cluster groups, we used a linear mixed effects model (LME) (Bates et al., 2015) in the `nlme` package (Pinheiro et al., 2017). To account for temporal autocorrelation of the daily activity data, we used an autoregressive correlation (AR(1)) structure. The proportion of the day the logger was wet was logit

transformed to obtain approximately normal distributions. All models had Bird ID as the random term and a Gaussian family distribution and the model fit was estimated using maximum likelihood.

Spearman's rank correlation coefficients were used to examine if environmental variables were correlated. Variables were weakly correlated, in all cases (r_s <0.5), so all variables were included in analyses. To assess the long-term trends of marine environmental variables (Chl *a*, SST, SSH, SSHa) in the 50% KUD area (core foraging region) used by each group, generalised linear models (GLM) were used. Using the `MuMin` package the best models were elected using Akaike's Information Criteria (AIC) (Burnham and Anderson, 2002) and Akaike's weight, using the small sample size correction (AICc). All analyses were conducted in R 3.4.0 for Mac OS X (R Development Core Team, 2016). Unless otherwise stated means ± standard deviation (s.d.) are presented.

Results

Migratory pathways and non-breeding distribution

Carrying a GLS device did not influence the return body masses of tracked birds (567.8 ± 51.6 g) when compared with those of control birds (572.0 ± 49.3 g, t = -0.46, df = 113.3 p = 0.65). The onset of migration varied by up to four weeks between individuals and typically commenced between 3 to 29 April. Birds dispersed upon reaching the North Pacific; utilising the Sea of Japan, the Sea of Okhotsk, the North Pacific Ocean, the Bering Sea, the Gulf of Alaska and the Chukchi Sea (Figure 2.1).

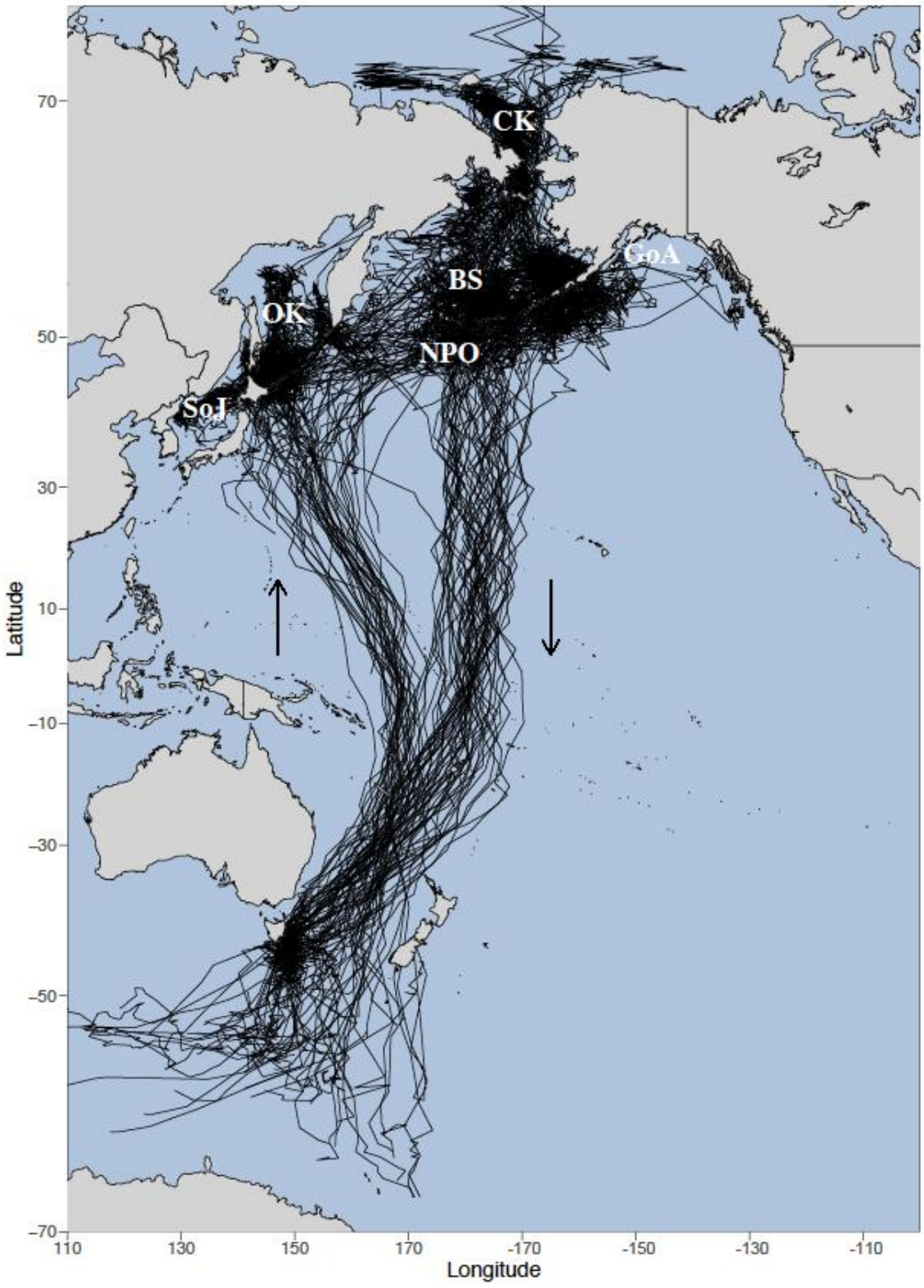

Figure 2.1. The post-breeding movements (April - October) of 60 short-tailed shearwaters tracked from Wedge Island (2012 - 2016). Arrows indicate direction of travel. SoJ = Sea of Japan, OK = Sea of Okhotsk, BS = Bering Sea, CK = Chukchi Sea, GoA = Gulf of Alaska.

Individual spatial foraging distribution

Cluster analysis identified two groups of birds that had similar spatial usage patterns of grid cells (Figure 2.2). The KUD analyses showed that the birds used distinct areas of the non-breeding regions, defined here as the Western and Eastern groups (Appendix 2.2). Based on the 50% KUD core ranges the Western group (n = 25) on average had 61 ± 21% of their locations associated with the Sea of Japan/Sea of Okhotsk and the North Pacific Ocean (Figure 2.3). The Eastern group (n = 35) had 64.3 ± 20.0% of their locations associated with the southeast Bering Sea, the Aleutian Islands and Bristol Bay (Figure 2.3). Except for 4 individuals, birds in the Eastern group did not forage in the Western region (Sea of Japan/Okhotsk Sea); instead they predominantly travelled in an easterly direction upon reaching the North Pacific. The number of days taken to migrate, days spent in the non-breeding region, and the most northerly location the birds moved to was similar between groups ($p > 0.05$ in all cases).

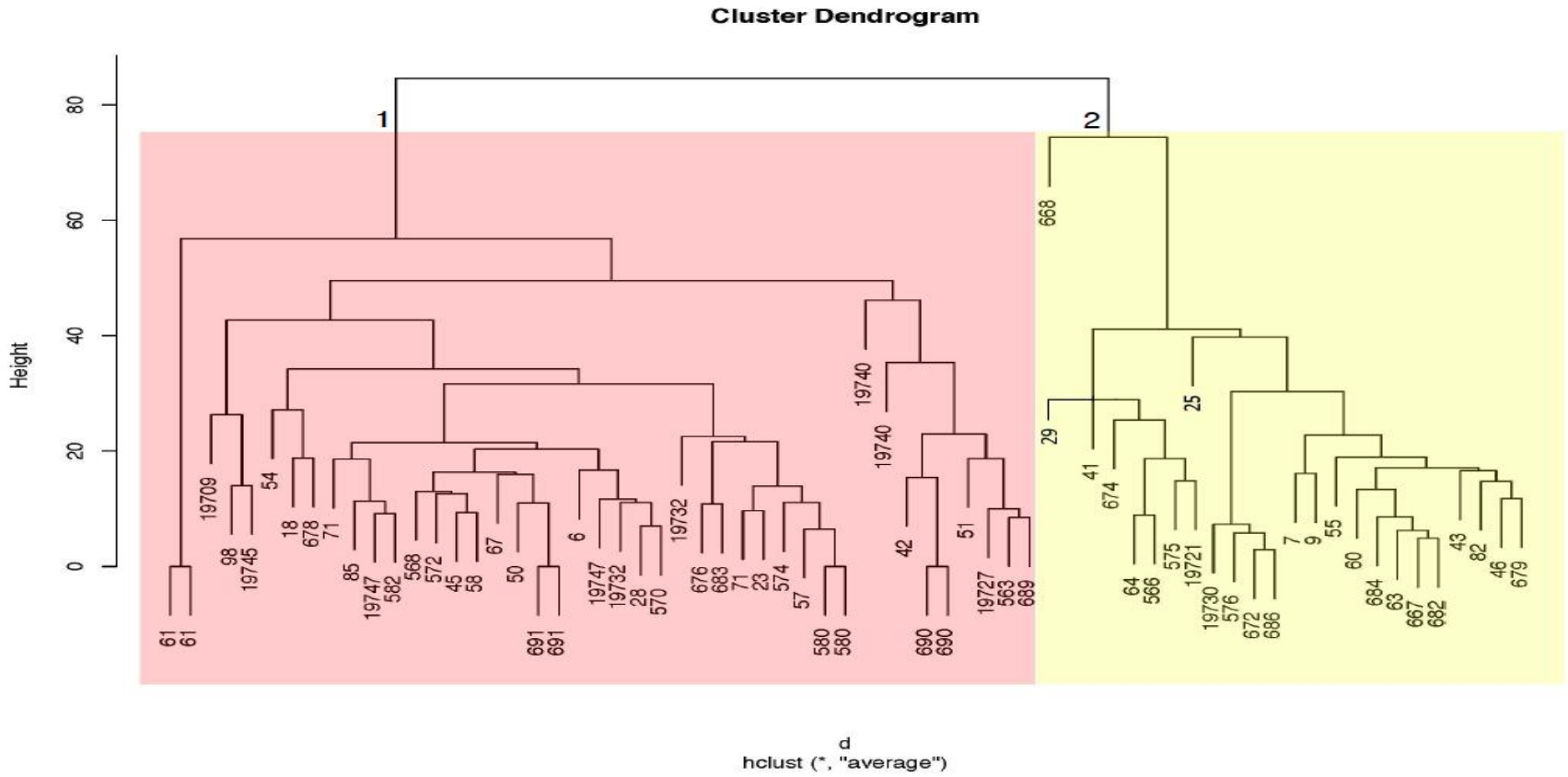

Figure 2.2. Cluster groups of short-tailed shearwaters from Wedge Island during the non-breeding period (2012 – 2016), determined by Ward's minimum variance method: 1) Eastern group (southeast Bering Sea/North Pacific; and 2) Western group (Sea of Okhotsk/North Pacific Ocean).

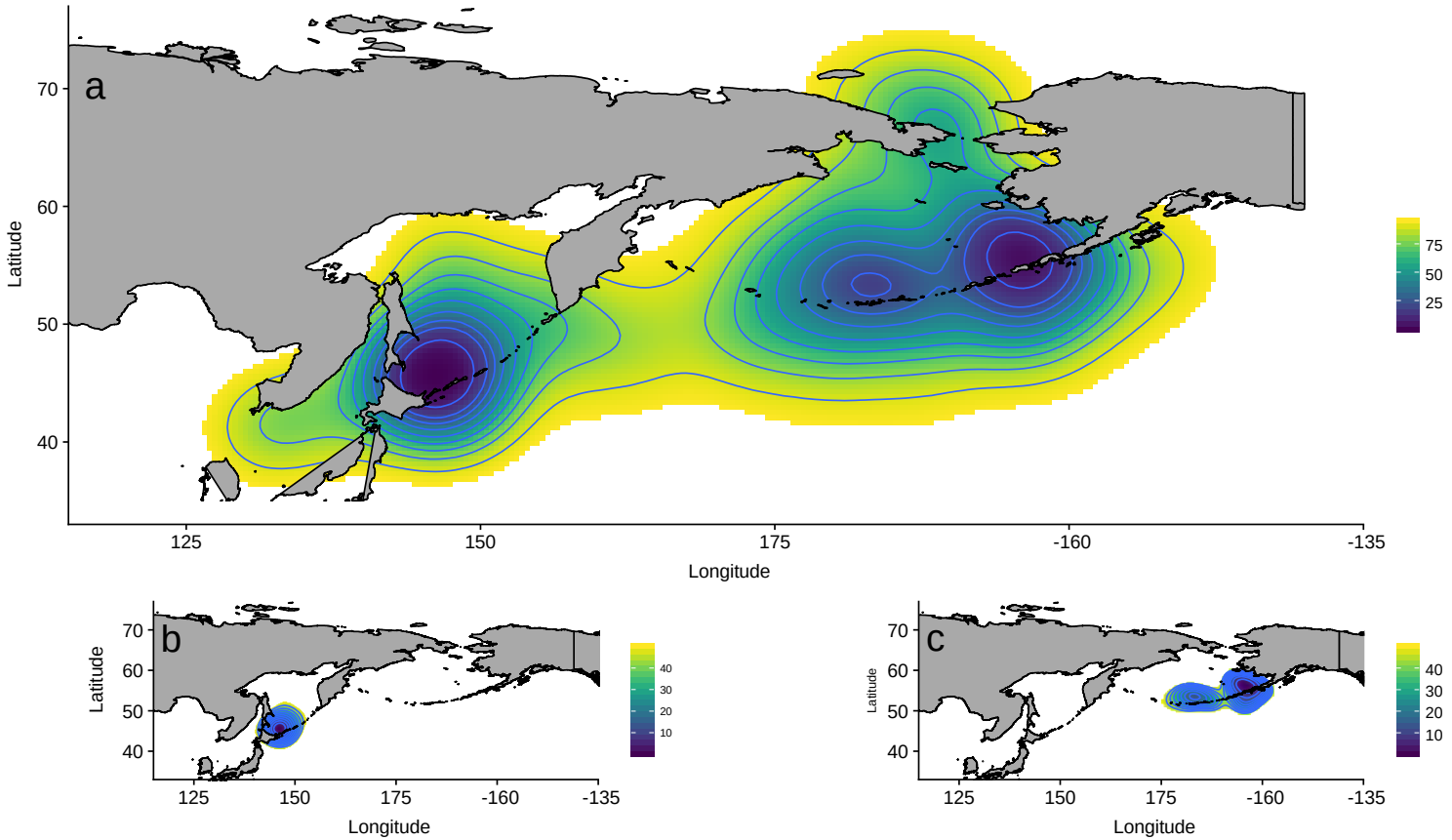

Figure 2.3. a) The 95% KUD home range of 60 short-tailed shearwaters tracked from Wedge Island, during the non-breeding season (2012 - 2016); and the 50% kernel KUD core foraging areas for; b) The Western group (n = 25); and c) the Eastern group (n = 35).

Within-season foraging movements

The proportion of time birds stayed within their core region varied between individuals but not among groups ($F_{1,66}$ = 0.90, P = 0.37) (Western 60 ± 20%; Eastern 64.3 ± 20% Table 2.2). Overall, birds spent between 15 and 99% (62.8 ± 20) of the non-breeding stage in their core regions (Appendix 2.3). Eight birds from the Western group first moved into the Sea of Japan upon reaching the North Pacific, where they spent between 26 to 46 days before moving to the Sea of Okhotsk. Of the Eastern group, 4 birds spent between 3 to 8 weeks foraging in the Western core area (Sea of Okhotsk, Sea of Japan, Kuril Islands and eastern Japanese coastline) before moving to the Eastern core foraging area in the southeast Bering Sea. Of the Eastern group, 3 birds foraged (>4 weeks) in the eastern North Pacific/Gulf of Alaska following their arrival and then moved back into the Eastern core region. By the end of August, 10 Western birds and 20 birds from the Eastern group shifted to the Chukchi Sea, where they remained (mid-August – early-September) until they commenced the southern migration (Figure 2.4). Further, 2 birds from the Western group and 3 birds from the Eastern group shifted to the North Bering Sea/Bering Strait in August.

Table 2.2. The number of days short-tailed shearwaters took to migrate, the number of days spent in the non-breeding region and the most northern point visited by birds (latitude) and the proportion (%) of the non-breeding stage that was spent in the core 50% KUD region by birds in each group. All values are mean ± SD.

Region	Northern migration	Southern migration	Non-breeding stage	Northern latitude (°)	Proportion of time (%) spent in core foraging area	n
Western	10.9 ± 2.8	12.8 ± 3.6	144.5 ± 12.7	62 ± 9.2	60 ± 20	25
Eastern	11.4 ± 4.8	12.5 ± 4.4	149 ± 12.2	67 ± 5.7	64.3 ± 20	35

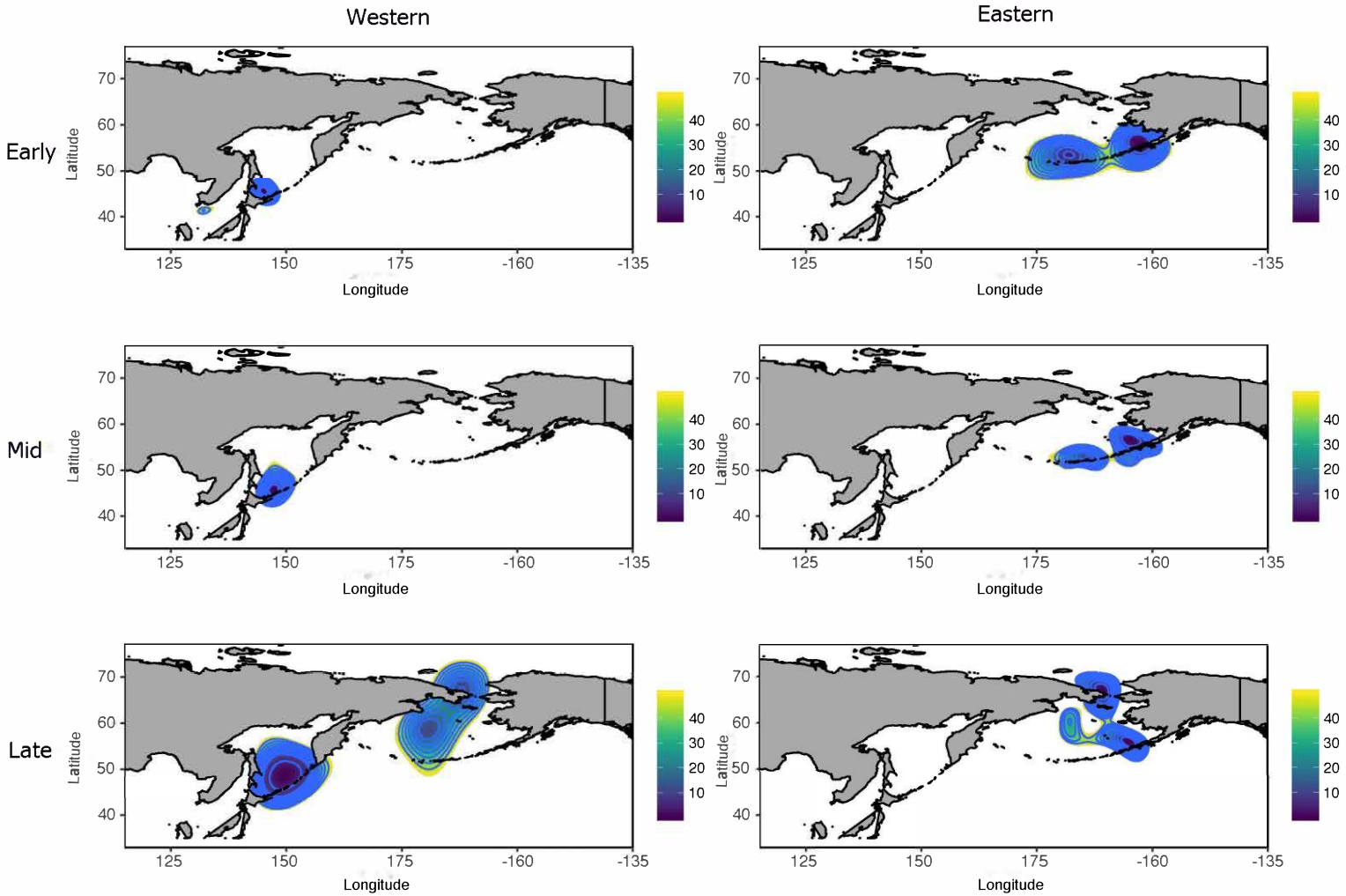

Figure 2.4. The seasonal distribution (50% KUD) of short-tailed shearwaters in the Western and Eastern core foraging areas during the non-breeding stage. Early (May - June), Mid (July - August) and Late (September - October).

Foraging site fidelity

Cluster analysis grouped the eight birds 061, 071, 580, 690, 691, 19732, 19740, 19747, which were tracked for two consecutive years into the Eastern core area in both years. Further examination of the track data confirmed that the birds had broadly overlapping core foraging regions in both years (Figure 2.5). However, the timing of arrival into the core area, the number of days spent in the core foraging region and the western and northern extents they reached varied between years.

Bird 061 travelled directly to the Eastern core area where it spent 32% of the non-breeding stage in 2015 but spent ~4 weeks in the North Pacific and Gulf of Alaska before shifting to the Chukchi Sea in early October. In 2016, 061 spent proportionally more time in the Eastern core region (72%) but it also spent time in the North Pacific and the northern Bering Sea. Bird 071 travelled to the Gulf of Alaska in 2013 and foraged in this region for ~1 month and then foraged in its core foraging region (66% of the non-breeding stage). In 2014, it spent 60% of the non-breeding stage in the eastern core area before moving north to the Chukchi Sea in late August. Bird 580 spent most of the non-breeding stage in the Eastern core area (66% in 2015; 66% in 2016) but shifted to the Chukchi Sea in both years. Bird 690 upon completing the northern migration spent ~4 weeks foraging within the Sea of Japan, Sea of Okhotsk and the Kuril Islands before moving to its Eastern core area where it spent 43% of the non-breeding stage before moving to the Chukchi Sea prior to the southern migration in 2015. In 2016, 690 spent ~1 week near the Kuril Islands before moving slowly towards the Eastern core area (50%) and moved to the Chukchi Sea prior to the southern migration in 2016. Bird 691, spent ~2 weeks foraging in the Sea of Okhotsk and Kuril Islands region before reaching the Eastern core region (90%) in 2015. In 2016, it spent ~5 weeks in the Sea of Okhotsk and Kuril Islands prior to reaching the Eastern core region (50%) and later moved to the Chukchi Sea prior to the southern migration in 2016. Bird 19732 spent the majority of both the 2012 (66%) and 2013 (60%) seasons in the Eastern region except for when it shifted north to the Chukchi Sea in late August in both years. Bird 19740 first foraged in Sea of Okhotsk and near the Kuril Islands (~2 months) prior to reaching the Eastern region (16%) and before moving to the Bering Strait mid-August in 2012. In 2013, after arriving into the North Pacific, 19740 spent ~3 weeks in the Sea of Japan prior to proceeding to its core

foraging area in the Eastern region (26%) but shifted to the Bering Strait in late August. Bird 19747 was faithful to the eastern Bering Sea during 2012 (90%), but in 2013, it spent less time in the Eastern region (76%) as it foraged within the Gulf of Alaska and the Chukchi Sea.

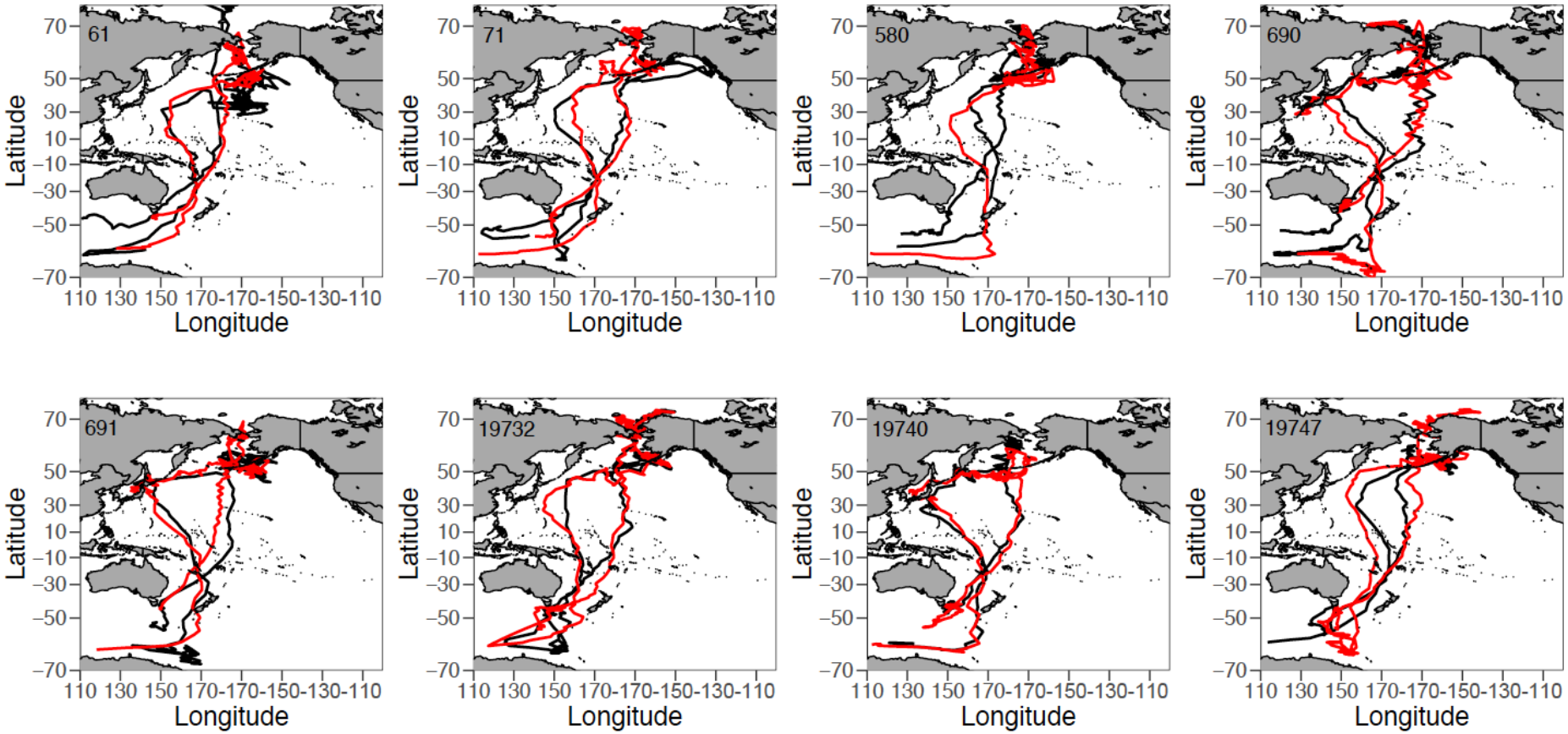

Figure 2.5. Repeat migration of eight short-tailed shearwaters between their breeding colony in Tasmania and the North Pacific Ocean. 061 (2015/black and 2016/red), 071 (2013/black and 2014/red), 580 (2015/black and 2016/red), 690 (2015/black and 2016/red), 691 (2015/black and 2016/red), 19732 (2012/black, 2013/red), 19740 (2012/black, 2013/red), and 19747 (2012/black, 2013/red).

Foraging effort among specialist groups

The proportion of time in the water (*pwet*) in the core 50% KUD regions was similar for each group (AIC_c, wi=0.9) (Table 2.3). The Western group spent 71 ± 22% *pwet*, and the Eastern group spent 66 ± 24% *pwet*.

Table 2.3. Linear Mixed Effects models for determining the relationship between the time the Western and Eastern groups of short-tailed shearwaters spent in the water (*pwet*) during the non-breeding period.

Candidate models	LogLik	AIC_C	ΔAIC	wAIC
1. Null	-6929	13864.1	0	0.6
2.Group~*pwet*	-6928.6	13865.1	1.03	0.4

Top model is bold

pwet = proportion of time the logger was wet.

LogLik, Log Likelihood, ΔAIC_C is the difference in AIC of the models to the best fitting model wAIC, indicates the probability of the best model.

Relationship between environmental variables and core foraging areas

Most environmental variables were similar between regions during the study period (May - September 2012 - 2016) although SST was ~2 °C warmer in the Western core area (Appendix 2.4). SST increased over time (1983 - 2016) (AIC_c, wi=0.7) (Figure 2.6 & 2.7). Neither region or year were found to influence mean annual Chl *a* (2003 - 2016) (AIC_c, wi= 0.5) (Table 2.4; Figure 2.6). Over time, SSH and SSHa (1993 - 2016) trended upwards in both foraging regions (Figure 2.6 & Figure 2.7). However, SSH varied between regions and years (AIC_c, wi=0.4) and SSHa varied between years but not regions (AIC_c, wi=0.5). Chl *a* showed distinct seasonal pattern in both regions (May - October 2003 - 2016). In the Eastern region Chl *a* was highest during May and gradually declined through October, whereas the Western region had two peaks in May and October (Appendix 2.5).

Table 2.4. Generalized Linear Model (GLM) results for examining the relationship between region, year and environmental variability.

Candidate models	DF	LogLik	AIC_C	ΔAIC	wAIC
Chla					
1. null	**2**	**18.3**	**-32.2**	**0.0**	**0.5**
2. Chla~region	3	18.8	-30.7	1.5	0.2
3. Chla~year	3	18.4	-28.1	2.4	0.2
4. Chla~region+year	4	18.9	-28.1	4.1	0.1
SST					
1. SST~region+year	**4**	**-52.2**	**113.0**	**0.0**	**0.7**
2. SST~region+year+region:year	5	-51.7	114.3	1.4	0.3
3. SST~region	3	-61.6	129.6	16.7	0.0
4. SST~year	3	-126.7	259.7	146.8	0.0
SSH					
1. SSH~region+year+region:year	5	129.1	-246.7	0.0	0.6
2. SSH~region+year	**4**	**127.2**	**-345.6**	**1.2**	**0.4**
3. SSH~year	3	120.2	-233.9	12.8	0.0
4. SSH~region	3	114.4	-222.2	24.5	0.0
SSHa					
1. SSHa~year	**3**	**127.3**	**-248.0**	**0.0**	**0.5**
2. SSHa~region+year	5	129.1	-246.8	1.2	0.3
3. SSHa~region+year+region:year	4	127.3	-245.6	2.4	0.2
4. null	2	114.4	-222.2	23.5	0.0

Top models are in bold

Chl *a*= chorophyll *a* (May - September 2003 - 2016); SST = sea surface temperature (May - September 1983 - 2016); SSH= sea surface height (May - September 1993 - 2016); SSHa = sea surface height anomaly (May - September 1993 - 2016). LogLik, Log Likelihood, ΔAIC_C is the difference in AIC of the models to the best fitting model. wAIC, indicates the probability of the best model.

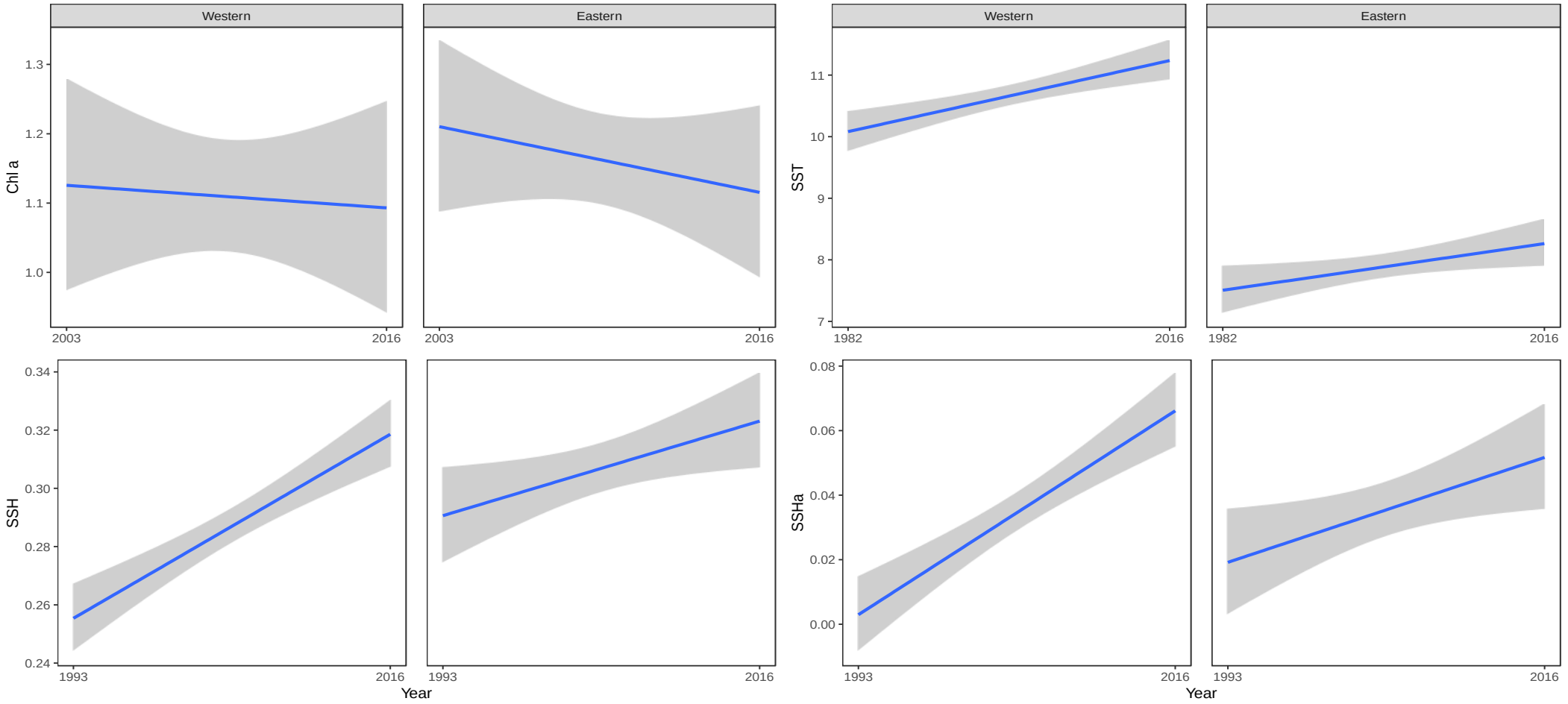

Figure 2.6. The relationship identified by Generalized Linear models between; a) chlorophyll *a* (Chl *a*; 2003 - 2016); b) sea surface temperature (SST; 1982 - 2016); c) sea surface height (SSH; 1993 - 2016); and d) sea surface height anomaly (SSHa; 1993 - 2016) and year and the core foraging regions used by short-tailed shearwaters during the non-breeding stage. 95% confidence interval is indicated by the grey shading.

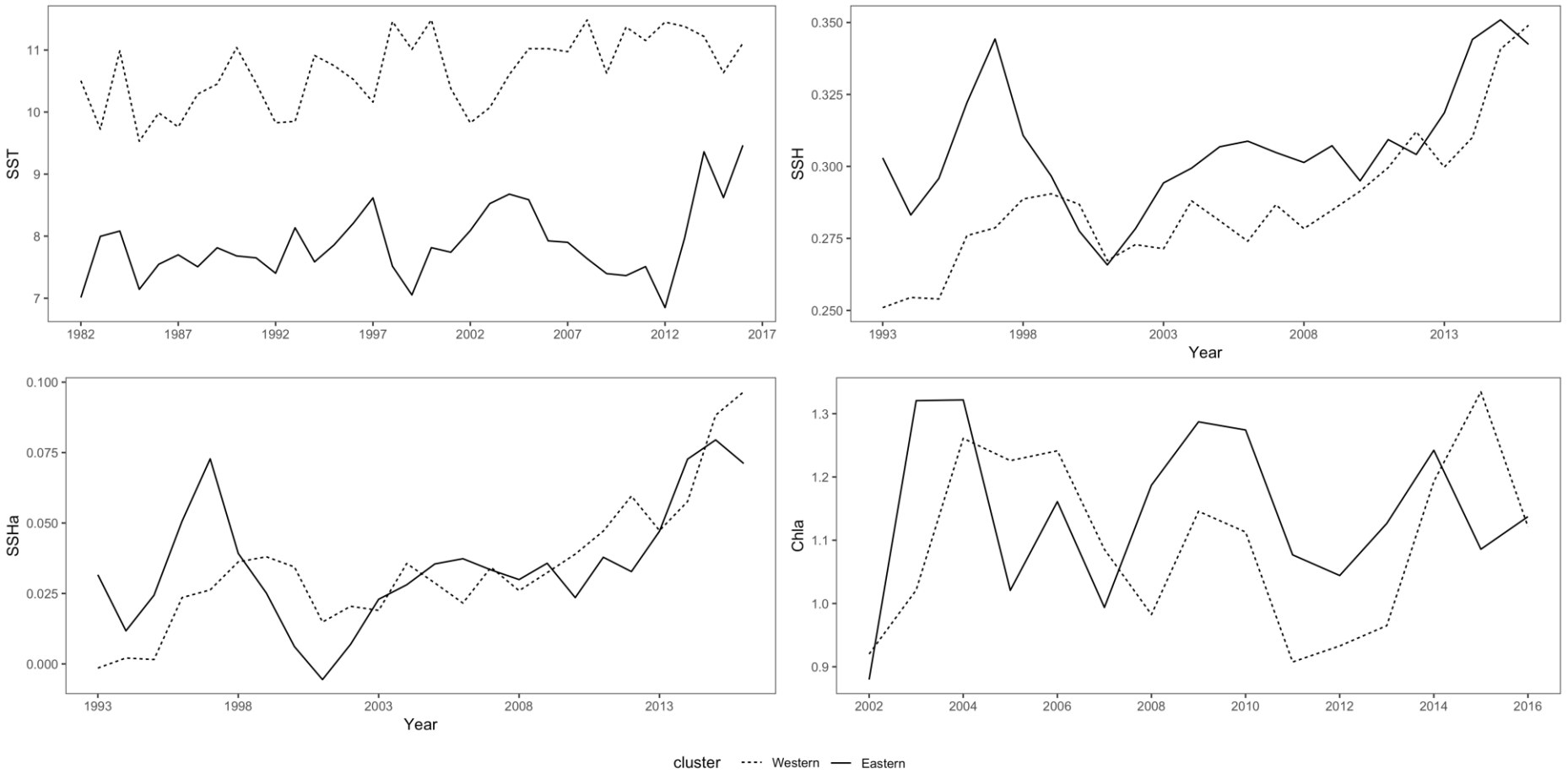

Figure 2.7. Environmental variables for the regions utilised by the groups of tracked short-tailed shearwaters during the non-breeding period (May - September): a) sea surface temperature (SST, 1982 - 2016); b) sea surface height (SSH, 1993 - 2016); c) sea surface height anomaly (SSHa, 1993 - 2016); and d) chlorophyll *a* (Chl *a*, 1993 - 2016).

Discussion

Birds were found to use two primary foraging regions: the Sea of Okhotsk/North Pacific Ocean (Western group, 42%), and the southeast Bering Sea/North Pacific (Eastern group, 58%). Individuals tracked for two consecutive years returned to the same core regions in both years. These regions likely provide a predictable supply of prey at the migration terminus allowing birds to quickly refuel. However, despite the propensity for individuals to use either the Eastern or Western regions, birds displayed variability in faithfulness to their core areas. This suggests that in order to maintain optimal rates of energy gain through the non-breeding stage, individuals balance the time spent within their core area with foraging success (Stephens and Krebs, 1986). The marginal value theorem (MVT) is founded on the assumption that as the rate of food intake declines compared to the long-term average, individuals should move to a new patch (Charnov, 1976). The individual shifts to the Chukchi Sea in this study coincided with seasonally declining Chl *a* concentrations in the core areas. The increasing abundance of large zooplankton in the southern Arctic in recent decades is likely providing short-tailed shearwaters the opportunity to broaden their foraging niche (Gall et al., 2013) which will be important given the environmental changes that are occurring in the North Pacific (Brown et al., 2011, Duffy-Anderson et al., 2017, Paik et al., 2017).

Within population foraging strategies

Except for four Eastern individuals, birds that utilised the Eastern core area did not forage in the Sea of Japan/Sea of Okhotsk, and *vice versa*. Although we did not determine the sex of birds, it is unlikely that the differing spatial habitat utilisation is a result of sex specific habitat requirements given males and females display similar migratory behaviours (Carey et al., 2014). Instead, birds most likely select where to forage based on past experiences, as most individuals directly navigated to their core foraging area. Also, those birds that were tracked for two seasons, returned to the same core area in both years. This tendency could be widespread in the population as Yamamoto et al. (2015) also found that short-tailed shearwaters used the same core habitat among years and that the centres of foraging activity were in the same regions used by our study birds.

For long-lived species, like short-tailed shearwaters, an extended immature phase (Skira, 1991) allows individuals to thoroughly explore non-breeding foraging habitats, which can lead to foraging site specialisations as individuals acquire knowledge of where the best places to find food are (Guilford et al., 2011, Missagia et al., 2015, Wakefield et al., 2015). Familiarity of the physical features of an area should increase foraging success (Irons, 1998) through better resource acquisition and assimilation, which is especially important after the birds' long migration over the less productive waters of the central Pacific (Baduini et al., 2001b). Additional costs associated with the energy required for flight feather synthesis during moult shortly after arrival place further pressure on birds to find food at this time (Hedenström and Sunada, 1999, Lindström et al., 1993). Therefore, when animals must immediately find food, rather than search for prey in areas in which they are naïve, returning to familiar areas where prey can be predictably located could reduce searching time and improve prey encounter rates (Irons, 1998).

Proportion of time spent in core foraging regions

The overall time spent in the core foraging areas and the time spent in the water (in this case a proxy for time spent foraging) was similar between groups. The mean Chl *a*, SSH and SSHa in the core areas were similar over the course of this study (2012 - 2016); and although SST was warmer in the Western region, those birds had similar proportions of within-season site fidelity to Eastern birds. However, there was considerable variability in the time birds spent within their core foraging region. Several of the individuals from the Eastern group foraged in the western North Pacific prior to reaching the Eastern core region. The lipid reserve of short-tailed shearwaters is likely depleted following the migration and so birds would need to regain mass to avoid starvation (Baduini et al., 2001b). The birds which foraged en route to the Eastern region may have arrived into the Northern Hemisphere with low lipid reserves, which could have prompted them to 'stopover' and feed before continuing to the Eastern core region (Baduini et al., 2001b, Goymann et al., 2010). Although, considering that four birds, including three of the birds which were tracked for two years, first utilised the Western core area (for up to 8 weeks) at the migration terminus suggests that some individuals may be familiar with both the Western and Eastern core areas, and consequently have a more diversified foraging strategy.

Secondary foraging regions

The timing of the birds' movements corresponded approximately with the seasonal cycle of primary production in the core foraging regions. Typically increasing daylight hours, rising spring temperatures and sea ice retreat initiate spring phytoplankton blooms (Hirota and Hasegawa, 1999, Kasai and Hirakawa, 2015, Liu et al., 2004, Saito et al., 2002) and this coincides with the arrival of migrating short-tailed shearwaters. Toward the end of the non-breeding stage (mid - late August) 50% of short-tailed shearwaters left their core foraging region and moved northwards to the North Bering Sea and the Chukchi Sea. This move coincided with the seasonal decline of Chl *a* concentrations in the core foraging areas. Typically, in the southeast Bering Sea, there are seasonal shifts in the distribution of shearwaters' prey, such as Euphaussid *spp.* and sand lance (*Ammodytes hexapterus*) from inshore/inner-shelf areas to offshore through early spring to late summer and this progression has previously been closely associated with the distribution of shearwaters (Hunt et al., 2014, Jahncke et al., 2005). Likewise, the density of short-tailed shearwaters has been found to be in synchrony with the late summer seasonal availability of large bodied krill in the Chukchi Sea (Nishizawa et al., 2017). Our findings suggest that changes in environmental conditions prompt birds to leave the core foraging areas and move to more northern latitudes. Long-tailed skuas (*Stercorarius longicaudus longicaudus*) (van Bemmelen et al., 2017), brown skuas (*Catharacta antarctica*) (Krietsch et al., 2017), and the yelkouan shearwater (*Puffinus yelkouan*) (Raine et al., 2013) also employ a similar strategy during the non-breeding stage; individuals return to the same sites among years but shift with changing local environmental conditions.

Temporal environmental trends in the core foraging regions

There was a gradual annual increase in SST (0.03°C; 1983 - 2016), SSH (0.002; 1993 - 2016), and SSHa (0.002; 1993 - 2016), but a slight annual decrease in Chl *a* (-0.005; 2003 - 2016) in the core foraging regions. Overall, SST was warmer in the Western core area (0.02 °C increase annually), but the increase in SSH and SSHa over time was similar between regions. The increase in SST in the core areas mirror the general warming trend of the North Pacific, which is significantly changing the dynamics of sea ice and primary productivity (Johannessen et al., 2004, Markus et al., 2009, Overland and Stabeno, 2004, Wood et al., 2015). Sea ice extent and duration have fluctuated significantly in the Bering Sea in recent

years but have remained relatively more stable (Brown et al., 2011, Frey et al., 2015) than sea ice in the Sea of Okhotsk and the Chukchi Seas where its extent and persistence have declined (Ogi et al., 2015, Paik et al., 2017, Stroeve et al., 2012). However, the observed changes in sea ice dynamics in the Chukchi Sea may benefit short-tailed shearwaters as warming temperatures are associated with higher primary productivity in this region (Brown and Arrigo, 2012, Brown et al., 2011, Grebmeier et al., 2006a), and this provides nutrients for subarctic zooplankton transferred north from the Bering Sea, subsequently increasing the overall abundance of zooplankton (Matsuno et al., 2011).

In contrast, reduced sea ice extent and warmer SST in the southeast Bering Sea, limits the spring phytoplankton bloom over the shelf (Duffy-Anderson et al., 2017). This is thought to deprive large bodied lipid rich zooplankton of ice algae, which is needed for reproduction and growth (Hunt et al., 2011, Sigler et al., 2014, Stabeno et al., 2012b). When warm stanza events occur in the Bering Sea, the reduction in zooplankton cascades up to higher trophic levels. Poor recruitment associated with declining meso-zooplankton abundance can cause walleye pollock (*Theragra chalcogramma*) stocks to decline (Coyle et al., 2011, Moss et al., 2009, Mueter et al., 2011). Thus, changing climate conditions are altering the food base (Carmack and Wassmann, 2006, Hunt et al., 2013), which short-tailed shearwaters and other marine predators rely upon.

Implications of individual foraging strategies in a changing climate

Based on the premise of optimal foraging theory, if resource availability is low then individuals should expand their niche (Stephens and Krebs, 1986). Therefore, short-tailed shearwaters likely return to sites where they were previously successful, but if the benefits of foraging in that patch declines, in order to maximise the net rate of energy intake, some individuals may ‘give up’ and move (Brown, 1988, Charnov, 1976). Travel costs may be compensated for in some years if movement from an individual’s core foraging area results in greater net energy gains. For example, during periods of anomalous climate conditions northern elephant seals (*Mirounga angustirostris)* that had low site fidelity performed better than individuals that maintained high fidelity (Abrahms et al., 2018), but high fidelity was more profitable when conditions were stable. Within a season, moving out of the core foraging area could help short-tailed shearwaters to deal with prey scarcity so long as they find alternative profitable foraging sites. The physical conditions within the core foraging

areas shearwaters use are changing. The environmental variables in these sites fluctuate year-to-year (e.g. SST) and presumably prey is not equal between the regions due to site-specific ocean dynamics. Consequently, a warming climate is likely to influence these regions differently.

Those individuals that continue to show fidelity to a foraging region may benefit when prey availability is high, but birds with a more flexible foraging strategy will be advantaged when resources are scarce (Phillips et al., 2017, Switzer, 1993). Long-term foraging site fidelity should act to maximise net energy gain over a life-time (Perry and Pianka, 1997), but if the productivity of a region progressively declines due to directional climate change then individuals that maintain fidelity to that region could experience diminished fitness (Hindell et al., 2017). However, the short-tailed shearwater population may be resilient to a changing climate because they use a wide range of foraging sites and they demonstrate plastic foraging behaviour. Further, increasing primary productivity and the persistence of open water areas in the Chukchi Sea, may present shearwaters with an alternative site if prey availability declines in their more southern foraging areas (Gall et al., 2017).

Although our results suggest that individuals could use the same core area for a number of years, the lack of data on individual strategies for longer than two years precludes drawing conclusions as to whether these strategies endure over the extent of a short-tailed shearwaters lifetime. How long the majority of migratory seabirds maintain among-year foraging fidelity when faced with continued change is unknown (Carneiro et al., 2017). There is some evidence that other seabirds repeatedly use the same non-breeding staging areas, such as Atlantic puffins (*Fratercula arctica*), which maintain divergent migratory routes over several years (Fayet et al., 2016a). Further, streaked shearwaters (*Calonectris leucomelas*), were found to maintain consistent migratory paths and demonstrated fidelity to winter staging areas among years (Yamamoto et al., 2014).

Short-tailed shearwaters are highly mobile, and sample their habitats over broad spatial scales, and they can consume a wide variety of prey (Baduini et al., 2006). They could therefore be more inclined to risk changing foraging strategies. Indeed, some common (*Uria lomvia*) and thick-billed murres (*Uria aalge*) switched core winter foraging areas after two to three years (Tranquilla et al., 2014). Further, Cory's shearwaters (*Calonectris diomedea*),

demonstrate extreme non-breeding foraging site plasticity as some individuals switch between ocean basins and hemispheres (Dias et al., 2011). The tendency of short-tailed shearwaters to leave their core foraging area within a season demonstrates that the foraging decisions of the birds are intertwined with conditions they encounter and the knowledge of alternative productive foraging sites, e.g. the Gulf of Alaska and the Chukchi Sea. It may eventuate that in years of low prey abundance, birds move between patches more readily to increase net energy gains. Potentially, if a bird continues to be unsuccessful in its core area over several years and it has had success at alternative sites, it may broaden its foraging range.

To determine whether short-tailed shearwaters expand their foraging niche when faced with continued change in their preferred habitat would require investigation of their foraging behaviour over a number of years. Further, assessing the fitness benefits/costs of the individual strategies is needed to quantify the long-term viability of the individual strategies, given the implications these may have for the overall population sustainability under the scenario of increasingly extreme climatic events in a changing environment.

Acknowledgements

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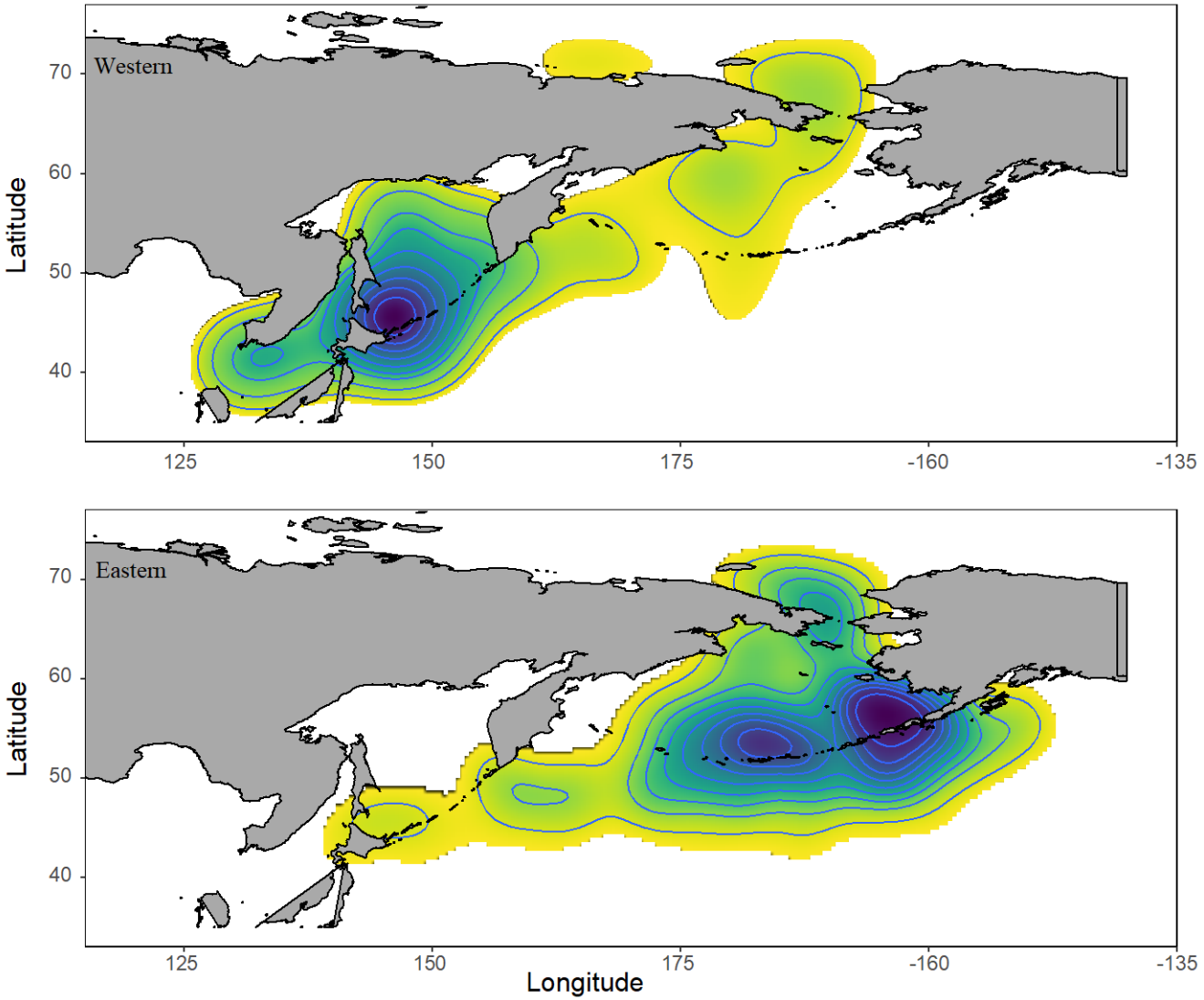
Appendices

Appendix 2.1. Deployment and recovery of Global Location Sensor loggers on short-tailed shearwaters at Wedge Island 2010 - 2016.

Deployed/Recovered	Breeding Season	October	November	December	January	February	March	April	Total Deployed	Total Recovered
Deployed	2010	17		13	20				**50**	
Recovered	2010			12	9	12				33
Recovered	2011			1						1
Recovered	2014							1		1
Sub - Total										**35**
Deployed	2011			22					**22**	
Recovered	2011						7			7
Recovered	2012	2	1	1	1					5
Recovered	2013		4 (2 NL)	1						5
Sub - Total										**17**
Deployed	2012	15			12		3	7	**37**	
Recovered	2012			3	3					6
Recovered	2013		6	3						9
Recovered	2014		1			1 (NL)				2
Recovered	2015	1 (NL)								1
Sub - Total										**18**
Deployed	2013			11			24		**35**	
Recovered	2013				1	4	3			8
Recovered	2014	15	8	1						24
Sub - Total										**32**
Deployed	2014		14	11		19	20	12	**76**	
Recovered	2014						6	7		13
Recovered	2015	20		17				2		39
Recovered	2016	5								5
Sub - Total										**57**
Grand - Total									**220**	**159**

NL = Logger had fallen off the bird prior to recovery.

Breeding Season = October to April. All tags were deployed and recovered during the breeding season.



Appendix 2.2. The 95% KUD of cluster groups (Cluster 2 = Western group - Sea of Okhotsk/North Pacific, and Cluster 1 = Eastern group - southeast Bering Sea/North Pacific) of short-tailed shearwaters during the non-breeding season (May - October 2012 – 2016).

Appendix 2.3. Summary of the non-breeding movements of short-tailed shearwaters from Wedge Island.

ID	Year	Foraging region	Commenced northern migration (DOY)	Finished northern migration (DOY)	Western longitude	Eastern longitude	Northern latitude	Time in core area (%)**	Mean time spent in the water (*pwet*) in core area (%)	Commenced southern migration (DOY)	Finished southern migration (DOY)**
6	2014	Eastern	118	128	170°E	151°W	65°N	74	55.7 ± 19.8	262	274
23	2014	Eastern	115	133	152°E	171°W	70°N	65	64.8 ± 22.7	269	281
42	2015	Eastern	105	114	158°E	155°W	71°N	65	62.9 ± 28.2	281	290
45	2015	Eastern	115	125	180°E	167°W	70°N	84	57.3 ± 24.9	270	282
51	2015	Eastern	116	125	163°E	165°W	70°N	49	47.3 ± 21.8	274	283
54	2015	Eastern	119	126	147°E	159°W	58°N	80	74.7 ± 21.9	271	283
58	2015	Eastern	111	127	148°E	159°W	80°N	71	61.5 ± 23.7	310	319
61	2015	Eastern	98	132	77°W	146°W	81°N	32	NA	303	316
61	2016	Eastern	102	111	165°E	157°W	64°N	72	NA	263	281
71	2013	Eastern	105	117	159°E	131°W	58°N	66	68.7 ± 20.4	274	284
71	2014	Eastern	106	117	160°E	156°W	70°N	60	NA	270	322
85	2013	Eastern	106	121	161°E	157°W	59°N	91	76.7 ± 20	272	287
563	2015	Eastern	117	126	164°E	160°W	67°N	60	67.1 ± 20	262	274
568	2015	Eastern	105	116	170°E	151°W	61°N	86	77.7 ± 19	270	281
572	2015	Eastern	109	125	141°E	153°W	59°N	80	62.2 ± 24.2	300	314
580	2015	Eastern	97	109	167°E	151°W	70°N	66	63.2 ± 24.2	271	285
580	2016	Eastern	107	115	167°E	158°W	70°N	65	NA	NA	NA
676	2015	Eastern	115	124	161°E	151°W	71°N	46	45.8 ± 21.7	271	282
683	2015	Eastern	116	126	151°E	157°W	70°N	47	49.7 ± 7.5	280	290
689	2015	Eastern	116	125	163°E	168°W	66°N	73	62.4 ± 20.1	271	281
690	2015	Eastern	114	126	131°E	164°W	71°N	43	69 ± 22.2	265	277
690	2016	Eastern	109	127	131°E	156°W	71°N	50	NA	264	280
691	2015	Eastern	117	125	136°E	153°W	69°N	90	67.1 ± 24.1	270	283

ID	Year	Foraging region	Commenced northern migration (DOY)	Finished northern migration (DOY)	Western longitude	Eastern longitude	Northern latitude	Time in core area (%)**	Mean time spent in the water (*pwet*) in core area (%)	Commenced southern migration (DOY)	Finished southern migration (DOY)**
691	2016	Eastern	104	114	131°E	157°W	69°N	50	NA	270	283
19727	2012	Eastern	117	127	156°E	152°W	71°N	58	NA	259	270
19732	2012	Eastern	115	126	178°E	150°W	72°N	66	NA	268	280
19732	2013	Eastern	105	125	174°E	153°W	72°N	60	NA	263	281
19740	2012	Eastern	102	117	151°E	174°W	69°N	16	NA	255	266
19740	2013	Eastern	105	115	130°E	166°W	60°N	26	NA	251	271
19745	2012	Eastern	101	113	164°W	147°W	56°N	50	NA	258	276
19747	2013	Eastern	117	130	155°E	158°W	72°N	76	NA	256	298
19747	2012	Eastern	106	115	157°E	141°W	59°N	90	NA	266	278
18	2013	Eastern	92	111	151°E	157°W	57°N	82	NA	264	276
28	2013	Eastern	118	129	180°E	158°W	72°N	73	66.3 ± 23.3	274	286
50	2015	Eastern	119	132	171°E	160°W	60°N	91	63.8 ± 23.9	271	284
57	2015	Eastern	116	127	150°E	156°W	71°N	56	58.8 ± 26.4	271	281
67	2014	Eastern	104	114	171°E	158°W	72°N	82	66.2 ± 24.3	273	283
98	2013	Eastern	106	118	161°E	153°W	56°N	70	NA	273	NA
570	2015	Eastern	102	112	77°W	154°W	71°N	74	66.9 ± 24.5	269	280
574	2015	Eastern	103	113	171°E	162°W	70°N	63	73.8 ± 20.4	270	280
582	2015	Eastern	99	110	160°E	136°W	63°N	75	79.8 ± 19.1	283	293
678	2015	Eastern	102	111	163°E	148°W	61°N	83	66.2 ± 26.5	270	280
19709	2012	Eastern	115	124	154°E	150°W	58°N	82	NA	264	273
7	2014	Western	104	115	140°E	174°W	62°N	76	NA	265	275
9	2013	Western	104	122	138°E	159°W	80°N	56	NA	287	295
25	2014	Western	114	127	140°E	164°E	55°N	57	76.1 ± 16.1	242	NA
29	2014	Western	117	128	140°E	164°W	63°N	54	84.6 ± 20.4	NA	NA
41	2015	Western	104	113	129°E	170°W	72°N	33	69.6 ± 22.2	271	282

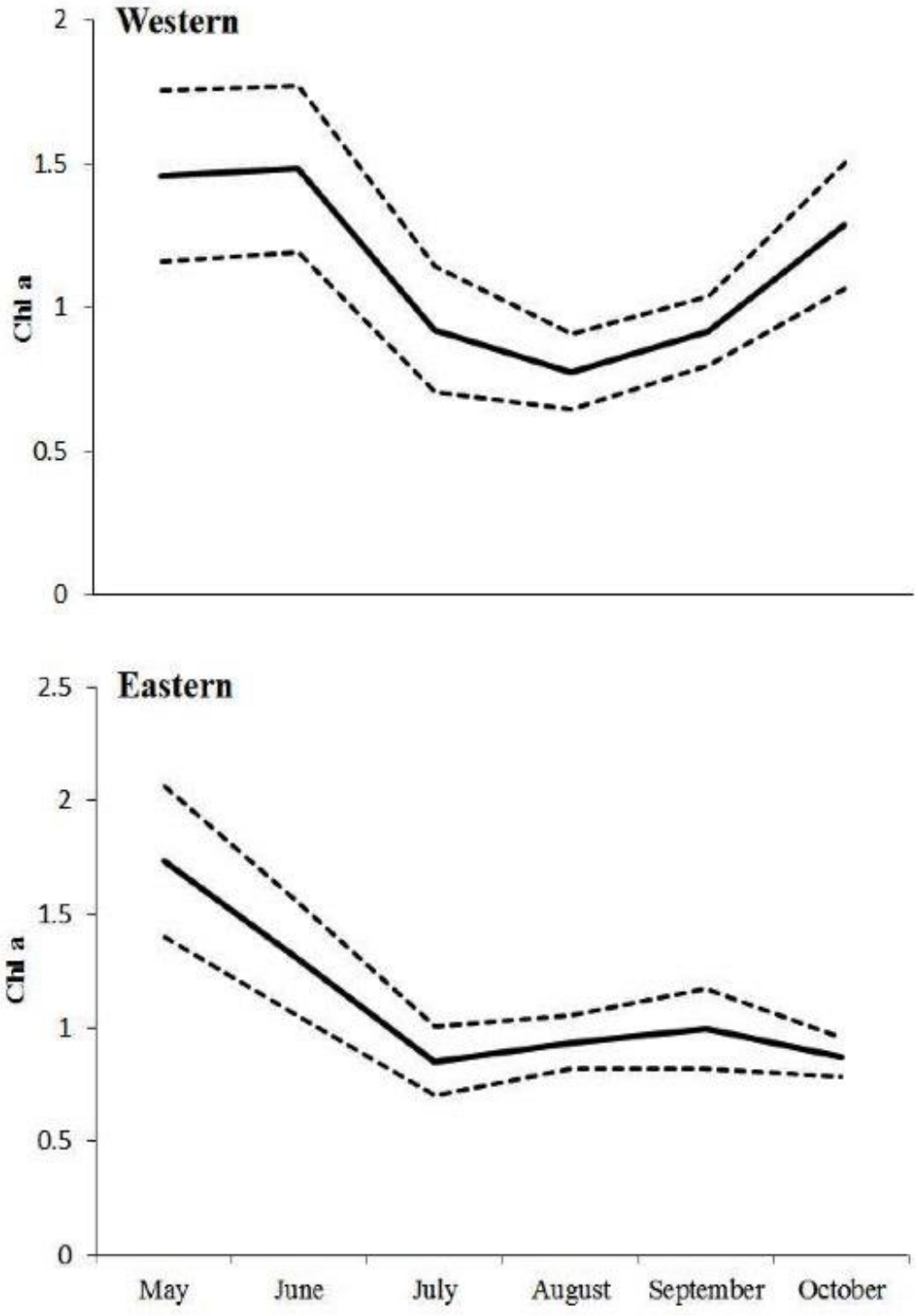
ID	Year	Foraging region	Commenced northern migration (DOY)	Finished northern migration (DOY)	Western longitude	Eastern longitude	Northern latitude	Time in core area (%)**	Mean time spent in the water (*pwet*) in core area (%)	Commenced southern migration (DOY)	Finished southern migration (DOY)**
43	2015	Western	118	127	133°E	178°W	61°N	71	67.9 ± 21.5	270	282
46	2015	Western	103	112	134°E	169°W	72°N	58	79.1 ± 10.1	264	274
55	2015	Western	117	125	143°E	167°W	70°N	62	74 ± 21	283	292
60	2015	Western	115	125	140°E	178°E	57°N	72	69.3 ± 22.6	265	276
63	2015	Western	114	124	140°E	167°W	65°N	70	67.9 ± 20.7	272	282
64	2015	Western	116	125	129°E	176°W	59°N	52	55.2 ± 18.9	264	273
82	2013	Western	108	123	132°E	172°W	57°N	58	79.2 ± 15	266	280
566	2015	Western	116	126	130°E	178°W	52°N	57	64.7 ± 26.1	260	283
575	2015	Western	100	110	129°E	179°E	57°N	40	64.1 ± 24.7	265	275
576	2015	Western	105	115	141°E	175°W	54°N	89	63.4 ± 25.2	270	281
667	2015	Western	118	127	138°E	168°W	70°N	77	49.9 ± 4.8	254	268
668	2015	Western	103	113	142°E	162°E	56°N	15	56.4 ± 23.3	270	283
672	2015	Western	116	127	141°E	152°E	52°N	95	75.5 ± 22.4	261	274
674	2015	Western	99	111	129°E	160°W	71°N	33	82 ± 16.3	254	267
679	2015	Western	106	118	132°E	156°W	72°N	56	77.1 ± 13.4	262	273
682	2015	Western	112	125	127°E	157°W	69°N	58	78.3 ± 19	273	285
684	2015	Western	115	128	140°E	177°W	62°N	57	80.7 ± 19.1	272	282
686	2015	Western	114	128	142°E	150°E	50°N	99	76.5 ± 21	268	279
19721	2012	Western	103	114	130°E	162°W	73°N	40	NA	272	279
19730	2012	Western	102	114	136°E	156°E	48°N	92	NA	258	280

** The proportion of days spent in core foraging areas calculated from the total days spent in the non-breeding region (> 40°N)

** The date birds 2, 29, 98 and 580 completed the southern migration was not available as their tags failed just prior to their return to the colony

Appendix 2.4. Environmental variables for each of the core regions short-tailed shearwaters used during the non-breeding season: a) 2012 - 2016; and b) long-term trends. Chlorophyll *a* concentration (Chl *a*, 2003 - 2016), sea surface temperature (SST, 1983 - 2016), sea surface height (SSH, 1993 - 2016), and sea surface height anomaly (SSHa, 1993 - 2016). Western = Sea of Okhotsk/North Pacific, and Eastern = southeast Bering Sea/North Pacific.

Variable	Region	Mean	Min	Max
a) 2012 - 2016				
Chl *a*	Western	1.1 ± 0.4	0.8	2.0
	Eastern	1.1 ± 0.3	0.7	1.7
SST	Western	11.2 ± 4.7	3.5	16.5
	Eastern	8.5 ± 2.8	3	12.2
SSH	Western	0.3 ± 0.04	0.3	0.4
	Eastern	0.3 ± 0.03	0.3	0.4
SSHa	Western	0.07 ± 0.04	0.02	0.1
	Eastern	0.06 ± 0.03	0.01	0.1
b) Long-term trends				
Chl *a*	Western	1.1 ± 0.1	0.9	1.3
	Eastern	1.1 ± 0.1	0.9	1.3
SST	Western	10.7 ± 0.6	9.5	11.5
	Eastern	7.9 ± 0.6	6.8	9.5
SSH	Western	0.3 ± 0.02	0.4	0.3
	Eastern	0.3 ± 0.02	0.3	0.4
SSHa	Western	0.03 ± 0.02	-0.001	0.1
	Eastern	0.04 ± 0.02	-0.006	0.1



Appendix 2.5. Mean monthly Chl *a* concentration for each of the core foraging regions (Western = Sea of Okhotsk/North Pacific, and Eastern = southeast Bering Sea/North Pacific) that short-tailed shearwaters used during the non-breeding season (May - October 2012 - 2016).

CHAPTER 3 IN RESPONSE TO CLIMATE VARIABILITY, SHORT-TAILED SHEARWATERS SHIFT WHERE THEY FORAGE RATHER THAN EAT LOWER TROPHIC PREY

Abstract

Large-scale climate anomalies can influence animal populations by changing the dynamics of the abundance and distribution of their prey. To better understand how climate variability influences the trophic position of the trans-equatorial migratory short-tailed shearwater (*Ardenna tenuirostris*), we used stable isotope analysis (SIA) to infer temporal trends in nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) values in relation to the Southern Annular Mode (SAM) over seven breeding seasons. The $\delta^{15}N$ and $\delta^{13}C$ values of birds upon their return from the North Pacific Ocean were enriched by ~4 ‰ compared to when they foraged in the Southern Ocean. Compound-specific stable isotope analysis of amino acids (AA-CSIA) showed that the baseline amino acid, phenylalanine, was enriched following the southern migration and gradually decreased through the breeding season. Thus, the gradual depletion of bulk $\delta^{15}N$ values were due to baseline differences in the Southern Ocean. $\delta^{13}C$ stable isotope values indicated that in response to the SAM, breeding adults travelled to areas of higher productivity rather than consume lower trophic prey. The trophic position of short-tailed shearwaters was not significantly different during a year of poor breeding success compared to a year of average breeding success. Therefore, variability in the quality and volume of meals fed to chicks could best explain breeding success fluctuations between years.

Introduction

Establishing how environmental variability influences temporal trends in diet is central to predicting how wildlife will respond to climate change in the future. In the ocean, climate anomalies influence primary productivity at local and basin-wide scales, which, through bottom-up processes, can reduce the resources animals rely on for survival and reproduction (Behrenfeld et al., 2006, Field et al., 1998). Climate anomalies within a season may immediately influence food web structure (Jakubas et al., 2016, Kowalczyk et al., 2014) while those enduring over extended periods can influence predator populations throughout the food web (Chambers et al., 2014, Baylis et al., 2015, Pomerleau et al., 2012). Monitoring variability in predator diet, as a proxy of the availability of lower trophic levels, allows assessment of whether climate variability affects the abundance of their food resources (Moody et al., 2012, Blight et al., 2015). In response to variability in the distribution and abundance of prey, predators may switch to alternative species or search for prey at different sites (Tarroux et al., 2016, Ambrose et al., 2013), which could affect breeding success (Ancona et al., 2012, Renner

et al., 2014). Therefore, to better understand how climate variability influences marine predator populations, identification of a species dietary range is required.

In the Southern Ocean, sea surface temperature and wind strength are strongly related to the Southern Annular Mode (SAM) (Thompson and Solomon, 2002, Thompson and Wallace, 2000), which directly influences oceanic productivity, upwelling and sea ice extent (Lovenduski and Gruber, 2005, Meredith et al., 2008). When the SAM is in a positive phase, the westerly wind belt contracts to the Antarctic (~65°S), which promotes upwelling and enhanced primary production in this region (Lovenduski and Gruber, 2005), whereas in the mid-latitudes (40-50°S) increased down-welling, lowered chlorophyll *a* concentration and warmer sea surface temperature (SST) occurs during a positive SAM phase. The SAM has been found to influence the production and abundance of phytoplankton (Saba et al., 2014), and macro-zooplankton (Steinberg et al., 2015). Therefore, protracted positive SAM phases (Marshall et al., 2004, Thompson and Solomon, 2002) may disrupt the transfer of energy to upper trophic predators in the mid-latitudes of the Southern Ocean. Indeed, the SAM has been the leading force influencing the breeding success and body condition of some Southern Ocean seabirds and seals (Massom et al., 2009, Weimerskirch et al., 2012, McMahon et al., 2017).

Bulk stable isotope analysis (SIA) is commonly used as a proxy to assess animal diet as nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope values reflect trophic level and habitat use respectively (Bond and Jones, 2009, Hobson et al., 1994). These isotopes deliver a time-integrated measure of prey assimilated into consumers in the order of days to months (Hobson and Clark, 1992, Bearhop et al., 2002). However, to accurately estimate the trophic level of consumers from stable isotope values and to compare between regions, knowledge of the isotopes at the base of the food web is required (Chikaraishi et al., 2009, Lorrain et al., 2009). Nitrogen isotopes in the form of particulate organic matter (POM) (e.g. algae and phytoplankton) vary at the base of the food chain both spatially and temporally (McMahon and McCarthy, 2016, Tamelander et al., 2009, O'Reilly et al., 2002). Therefore, the $\delta^{15}N$ values of those marine animals, which are migratory and forage over large areas, can vary due to these baseline differences (Richert et al., 2015, Newsome et al., 2010, Ramos and Gonzalez-Solis, 2012). Consequently, there can be a mismatch between bulk stable isotope

estimation of trophic level and the baseline values of $\delta^{15}N$ in the consumers diet (Cabana and Rasmussen, 1996).

Compound-specific isotope analysis of amino acids (AA-CSIA) can overcome the shortcomings of bulk SIA. This method can be used to estimate the trophic level of consumers using the values of two amino acids, phenylalanine (Phe) and glutamic acid (Glu). Phenylalanine retains the $\delta^{15}N$ signature from the base of the food web (McMahon and McCarthy, 2016, McClelland and Montoya, 2002). In contrast, Glu becomes enriched in $\delta^{15}N$ (~7‰ per trophic level) (McClelland and Montoya, 2002) relative to the diet providing an estimate of trophic transfer to the consumer (Chikaraishi et al., 2009). AA-CSIA compliments bulk stable isotope analysis as it not only provides a direct means to calculate trophic level but it also provides a measure of the source $\delta^{15}N$ in the consumers diet. This analysis ultimately helps to determine whether variability in $\delta^{15}N$ values identified by bulk SIA is attributed to consumption of prey across trophic levels, or whether the observed differences are due to baseline variability.

The short-tailed shearwater (*Ardenna tenuirostris*) is a wide-ranging pelagic predator (Connan et al., 2005, Cherel et al., 2005b) that breeds in the Southern Hemisphere but spends the non-breeding season in the North Pacific Ocean (Hunt et al., 1996). The ability of this species to forage over thousands of kilometres, across ocean basins from mid to high latitudes (Einoder et al., 2011, Yamamoto et al., 2015) makes them a good model species to use AA-CSIA to determine whether their $\delta^{15}N$ values differ due to baseline variability. In this study, we analysed $\delta^{15}N$ and $\delta^{13}C$ stable isotopes in the whole blood of short-tailed shearwaters to quantify seasonal trends in trophic position. Specifically we aimed to: 1) identify seasonal patterns in $\delta^{15}N$ and $\delta^{13}C$ values, 2) determine if variability in the Southern Annular Mode influences short-tailed shearwater trophic level, and 3) examine whether trophic level changes in diet influences breeding success.

Methods

Ethics statement

All animal handling and instrumentation was carried-out under Research Permits, Department of Primary Industries, Parks, Water and Environment (FA05151, FA10212, FA13009,

FA14063, FA15083, FA16077) and University of Tasmania Ethics Committee permits (A8138, A11338, A128942, A15572).

Study Site

Wedge Island (Southeast Tasmania, 43°07'S, 147°40'E) is located at the southern extent of the short-tailed shearwater's breeding range and supports a colony of approximately 20,000 - 25,000 breeding pairs. Blood samples were collected during the late-incubation and chick-rearing stages, January to March in 2005 to 2008, and for the entire breeding season from October to March in 2012 to 2014 (Appendix 3.1). The breeding season was divided into six stages (the date range and the number of samples collected for each stage are presented in parentheses): 1) *Post-migration* (October 3 - October 24, n = 56), 2) the *Pre-laying stage* (October 25 - November 20, n = 34), 3) *Early-Incubation* (November 21 - December 20, n = 55), 4) *Late-Incubation* (December 20 - January 20, n = 119), 5), *Early-chick rearing* (January 21 - February 28, n = 139), and 6) *Late-chick rearing* (March 1-March 31, n = 142). Within a breeding season, no individual was sampled more than once per stage. The breeding season is defined by the start year of the breeding season.

Sample collection

The half-life of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes in whole blood is 10 to 23 days for small organisms like short-tailed shearwaters (Hobson and Clark, 1993). In this study, isotopes collected from short-tailed shearwaters were considered representative of diet 20 ± 8 days prior to sampling. Therefore, samples collected at the beginning of October during the Post-Migration stage are considered representative of non-breeding season diet. Short-tailed shearwaters forage bi-modally during the breeding season. Food eaten from around the colony (short-trips) is fed to the chick (January - March) and feeding during this time does not assimilate into the adult's diet (Cherel et al., 2005b), so we assume that blood taken from adults represents diet from self-provisioning (long-trips) in the Southern Ocean. A small blood sample of ~1 ml was collected from the web vein of the foot using a 26-gauge needle and capillary tubes. During 2005 to 2008, blood samples were kept on ice until they were stored in a freezer at -20ºC on return from the field. In 2012 to 2015, blood samples were stored in 70% ethanol.

Ethanol does not contain nitrogen so it does not significantly alter $\delta^{15}N$ values (Hobson et al., 1997, Bugoni et al., 2008). However, storing samples in ethanol can alter $\delta^{13}C$ values in the blood sample (Bugoni et al., 2008, Ruiz-Cooley et al., 2011). This can occur as a result of hydrolysis of proteins during preservation, due to the extraction of lipids and also by contamination from the solvent itself (Carabel et al., 2009 and references within). However, not all studies have found that preservation of blood in ethanol alters $\delta^{13}C$ values (Hobson et al., 1997, Samarra et al., 2017). Inspection of the distribution of the data in this study showed variability between years in both groups that could not be attributed to the different preservation techniques (Appendix 3.2). Consequently, we did not separate the two groups for analysis.

Stable isotope analysis

We did not extract lipids, instead whole blood was used, as lipids in blood are generally low and lipid extraction can deplete nitrogen (Cherel et al., 2005a). The whole blood samples were dried at 60°C for 36 hours, powdered and placed into tin cups prior to analysis in a Micromass Isochrom (Manchester, UK) continuous-flow isotope-ratio mass spectrometer. Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is $\delta^{13}C$ or $\delta^{15}N$ and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Values were relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 (air) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors of 0.1 and 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Stable isotope analysis was conducted at the Stable Isotopes Laboratory, at the Environmental Biology Group, Research School of Biological Sciences Australian National University (ANU).

Compound specific stable isotope analysis of amino acids

To investigate whether changes in bulk isotope values were due to trophic shifts or because of regional baseline stable isotope variability changes, we analysed a sub-set of the samples using AA-CSIA. Samples for AA-CSIA were prepared following the method of Dale et al. (2011). Refer to Appendix 3.3 for further details on laboratory methods concerning AA-CSIA. To

establish whether the trophic position of prey consumed was different in a good year compared to a poor year, i.e. was poor breeding success a result of lower trophic prey, samples were selected from 2013 and 2014; two years of contrasting breeding success. At least two samples were selected per stage of the breeding season to allow comparisons between stages and years (n = 32).

All samples were analysed in triplicate. The $\delta^{15}N$ values were normalised as follows: each sample analysis consisted of three separate IRMS analyses bracketed by a suite of amino acids with known $\delta^{15}N$ values. The slope and intercept of known versus measured values were then used to correct the measured values for the sample set. Reproducibility associated with isotopic analysis of glutamic acid (Glu) and phenylalanine (Phe) averaged ± 0.44‰ (~1 SD) and ranged from ± 0.06‰ to ± 0.85‰ respectively.

Trophic position (TP) was calculated as follows (Hannides et al., 2009):

$$TP = \frac{\delta 15N_{Glu} - \delta 15N_{Phe} - \beta}{TDF} + 1$$

where β = the isotopic offset between Phe and Glu in primary producers (usually 3.4‰ in marine phytoplankton (McClelland and Montoya, 2002) and TDF is the Trophic Discrimination Factor. A TDF has not been calculated for short-tailed shearwaters. Preliminary analyses indicated that the TDFs developed by Chikaraishi et al. (2009) (7.6‰) and by Nielsen et al. (2015) (6.6‰), underestimated the TP of short-tailed shearwaters (~1 TP). Therefore, we used a TDF of 3.6‰ as this was the average $TDF_{Glu\text{-}Phe}$ calculated from the blood of four species of Southern Ocean penguins (Lorrain et al., 2009) and an avian-specific $TDF_{Glu\text{-}Phe}$ of 3.5‰ determined from captive gentoo penguins (*Pygoscelis papua*) fed a controlled diet (McMahon et al., 2015). As these species' diet overlaps with short-tailed shearwaters (i.e. they consume myctophid *spp*. and krill *spp*.), this value is likely to be more ecologically relevant than the broad species derived TDF of 7.6‰ as suggested by Chikaraishi et al. (2009).

Census and breeding success methods

The colony of short-tailed shearwaters at Wedge Island, was monitored from 2004 to 2016 as part of a long-term study investigating climate effects on the viability of the population.

Quadrats (2 m diameter) were permanently laid out in transects across the island in order to represent the different vegetation communities and the varying density of short-tailed shearwater burrows (1 - 21 burrows per quadrat). The content of each burrow within a quadrat was checked with a custom made burrow camera to ascertain whether a bird and an egg were present. For further details on the survey methods refer to Vertigan et al. (2012). To determine breeding success, burrows identified to contain an egg in December were inspected again in April, prior to chick fledging. Breeding success was defined as the proportion of chicks that were successfully raised from the number of eggs laid. Unforeseen logistical constraints prevented the chick census being carried-out in April 2012; hence breeding success data was not available for the 2011 breeding season. Due to the friable nature of the substrate in some sections of the colony, it was not always possible to survey all quadrats each year. Removal of the data for quadrats that could not be surveyed in some years resulted in 144 quadrats that were surveyed every year and these were used for analyses.

Environmental data

We quantified the relationship of bulk $\delta^{15}N$ and $\delta^{13}C$ stable isotopes between breeding stages and the SAM. The SAM data were downloaded from the Climate Data Guide (https://legacy.bas.ac.uk/met/gjma/sam.html) (Marshall, 2003). To compare the direct stage-specific effects of environmental variability and isotope values we used the monthly SAM data averaged from October to April i.e. the breeding season, for each year of the study.

Statistical analyses

Before analysis, data were assessed for normality and homoscedasticity and log transformed where appropriate. Inter-stage differences among bulk isotope $\delta^{13}C$ and $\delta^{15}N$ values were assessed using a General Linear Model (GLM) with log link functions. The best model was selected using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). The most parsimonious model was selected as the simplest model of those where $\Delta AIC \leq 2$. To determine whether AA-CSIA $\delta^{15}N_{phe}$ and $\delta^{15}N_{glu}$ values were associated with the stage of the breeding season and whether these values varied between years, we built Linear Mixed Effects models (LME) (Pinheiro and Bates, 1996). LME models were used to account for multiple replicates (2) per bird, with bird ID as the random effect, and compared to a null intercept only model which was fit by maximum likelihood using the `nlme` package (Pinheiro et al., 2017)

in R. Models were compared using a likelihood ratio test by Analysis of Variance (ANOVA). One-way ANOVAs were used to examine if breeding success varied between years.

Environmental models

Bulk stable isotope data were not available for the *Post-migration* to *Early-Incubation* stages in 2005 to 2008, so these stages (collected 2012 to 2014) were excluded from environmental models. Subsequently, only the *Late-Incubation, Early-chick rearing* and *Late-chick rearing* stages were included. General linear models (GLM) with a Gaussian family distribution with identity links were used to determine if variability in stable isotope signatures between stages were explained by the SAM. The best model was selected using Akaike's Information Criterion (AIC). All analyses were conducted in R 3.4.0 for Mac OS X (R Development Core Team, 2016). Means ± standard deviation (SD) are presented.

Results

Bulk $\delta^{15}N$ and $\delta^{13}C$

Bulk $\delta^{15}N$ values varied throughout the study period from 6.9 to 15.6‰ (9.1 ± 1.6) and $\delta^{13}C$ values ranged from -26.2 to -18.2‰ (-23.0 ± 1.8) (Appendix 3.1 & Appendix 3.4 & Figure 3.1). $\delta^{15}N$ and $\delta^{13}C$ values were associated with the stage of the breeding season (AIC_C, w = 1, in both cases) (Table 2). $\delta^{15}N$ and $\delta^{13}C$ were more enriched in the *Post-migration* stage compared to all other stages (GLM: t = 290.4 p< 0.0001) and (GLM: t = -138.7, p < 0.0001) respectively. Nitrogen and carbon values were correlated ($r^2 = 0.79$, p > 0.0001).

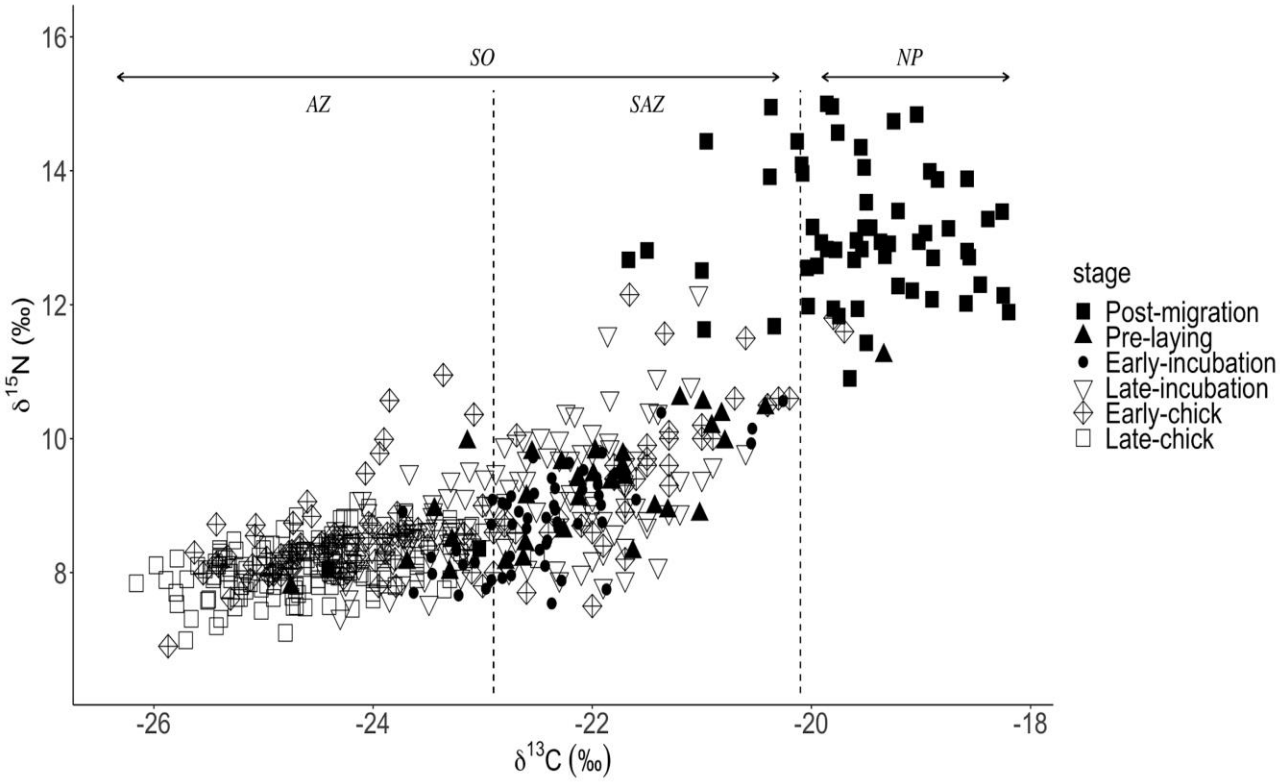


Figure 3.1. Bulk $\delta^{15}N$ and $\delta^{13}C$ values of short-tailed shearwaters from Wedge Island, by breeding stage. AZ = Antarctic Zone, SAZ = Sub-Antarctic Zone. Dashed lines indicate approximate biogeographic zones of the Southern Ocean, adapted from Phillips et al. (2009) and Jaeger et al. (2010). SO = Southern Ocean, NP = North Pacific.

AA-CSIA

Amino acid $\delta^{15}N_{phe}$ values ranged from -0.8 to 8.0‰ (1.9 ± 2.7) and $\delta^{15}N_{glu}$ values ranged from 15.3 to 24.3‰ (18.1 ± 2.2) (Table 3.1 & Appendix 3.5). Both $\delta^{15}N_{phe}$ and $\delta^{15}N_{glu}$ values were associated with the stage of the breeding season ($x^2(1) = 121.1$ $p < .0001$) and ($x^2(1)=142.4$ $p < .0001$) respectively. $\delta^{15}N_{phe}$ was enriched in the *Post-migration* stage (6.3 ± 0.8‰) compared to the breeding stages (0.5 ± 0.8‰). $\delta^{15}N_{glu}$ was also enriched in the *Post-migration* stage (21.2 ± 1.9‰) compared to all other stages (17.1 ± 0.9‰). However, trophic position calculated from $\Delta\delta^{15}N_{glu\text{-}phe}$ did not significantly vary between breeding stages ($x^2(1) = 6.9$ $p = 0.07$). *Post-migration* $\delta^{15}N$ values (4.2 ± 0.5) were enriched compared to the breeding stages (4.7 ± 0.3‰), indicating that baseline $\delta^{15}N$ values differ in the regions the birds utilised.

Breeding Season	Glu	Phe	Calculated Trophic Position	Bulk $\delta^{15}N$ ($^{0}/_{00}$)	Stage
2013	19.8 ± 1.1	5.8 ± 0.4	4.0 ± 0.4	12.3 ± 2.6	*Post-migration*
2014	22.1 ± 1.4	6.9 ± 0.8	4.3 ± 0.6	13.4 ± 1.1	*Post-migration*
2013	17.2 ± 0.5	-0.3 ± 0.2	4.9 ± 0.1	9.7 ± 1.8	*Pre-laying*
2014	17.6 ± 0.3	2.1 ± 0.8	4.4 ± 0.3	9.5 ± 0.1	*Pre-laying*
2013	16.8 ± 1.1	0.2 ± 0.6	4.7 ± 0.2	7.9 ± 0.2	*Early-incubation*
2014	17.7 ± 0.6	0.6 ± 0.7	4.9 ± 0.3	9.2 ± 0.7	*Early-incubation*
2013	16.4 ± 0.7	0.4 ± 0.6	4.5 ± 0.1	8.7 ± 0.6	*Late-incubation*
2013	17.1 ± 1.6	0.7 ± 0.3	4.6 ± 0.5	8.2 ± 0.1	*Early-chick rearing*
2014	16.7 ± 0.3	0.2 ± 0.4	4.7 ± 0.1	8.6 ± 0.0	*Early-chick rearing*
2013	16.6 ± 0.5	0.5 ± 0.1	4.5 ± 0.2	7.9 ± 0.2	*Late-chick rearing*
2014	17.5 ± 1.0	0.1 ± 0.8	4.9 ± 0.4	8.1 ± 0.2	*Late-chick rearing*

Table 3.1. Compound specific stable isotope analysis of glutamic acid (Glu) and phenylalanine (Phe), calculated trophic position and bulk $\delta^{15}N$ (‰) of the whole blood of short-tailed shearwaters from Wedge Island, by stage of the 2013 and 2014 breeding seasons. Mean ± SD are presented.

The influence of the SAM on $\delta^{15}N$ and $\delta^{13}C$ values

Both stage and the SAM were included in the model that best explained short-tailed shearwater $\delta^{15}N$ values (AIC_c, wi = 0.99) (Table 3.2). However, the sampling error associated with measuring stable isotopes in this study was 0.3‰ for $\delta^{15}N$ values. $\delta^{15}N$ values only varied by <= 0.3‰ in response to the SAM, which is equal to the sampling error, therefore it cannot be concluded that the SAM influenced $\delta^{15}N$ values (Figure 3.2).

The stage plus the interaction of stage with the SAM influenced $\delta^{13}C$ values (AIC_c, wi = 0.99) (Table 3.2, Figure 3.2). When the SAM was negative during the *Late-Incubation* stage $\delta^{13}C$ values were -21.9‰ compared to -22.9‰ when the SAM was positive. This pattern was also observed in the *Early-chick* and *Late-chick* rearing stages when $\delta^{13}C$ was higher when the SAM was negative in contrast to when it was positive, -22.6‰ compared to -23.9‰ and -24.1‰ compared to -24.8‰ respectively. Sampling error for $\delta^{13}C$ values were 0.1‰, thus indicating that the observed differences in $\delta^{13}C$ (> 1‰) values associated with the SAM reflect shifts in foraging location.

Table 3.2. a) Selection of models to determine inter-stage variability of bulk stable isotope values; and b) The influence of the SAM on bulk stable isotope values of short-tailed shearwaters at Wedge Island, by breeding stage.

a)	Model	logLik	AIC_c	ΔAIC	wi
$\delta^{15}N$					
	δ15N + stage	-685.4	1385.1	0	1
	Intercept	-1023	2050	664.8	0
$\delta^{13}C$					
	$\delta^{13}C$ + stage	-806.7	1628.5	0	1
	Intercept	-1078.8	2161.7	534.1	0
b)					
$\delta^{15}N$					
	$\delta^{15}N$ + SAM + stage	-675.5	1367.4	0.0	0.7
	$\delta^{15}N$ + SAM + stage + SAM*stage	-671.1	1368.9	1.5	0.3
	$\delta^{15}N$ + stage	-685.4	1385.1	17.7	0.0
	$\delta^{15}N$ + SAM	-1020.9	2047.8	680.4	0.0
	Intercept	-1022.9	2049.8	682.5	0.0
$\delta^{13}C$					
	$\delta^{13}C$ + SAM + stage + SAM*stage	-736.3	1499.2	0.0	1.0
	$\delta^{13}C$ + SAM + stage	-748.2	1512.6	13.4	0.0
	$\delta^{13}C$ + stage	-806.7	1627.5	128.3	0.0
	$\delta^{13}C$ + SAM	-1078.8	2161.7	662.4	0.0
	Intercept	-1078.3	2162.7	663.5	0.0

Note: logLik: log of the likelihood, the probability of the data given the model, AIC^c: Akaike's Information Criterion corrected for small samples sizes, ΔAIC: Akaike's Information Criterion, wi: Akaike weight. The "+" symbol indicates inclusion of a variable in the models without an interaction with other variables and the "*" symbol denotes interactions between variables. Top model is indicated in bold.

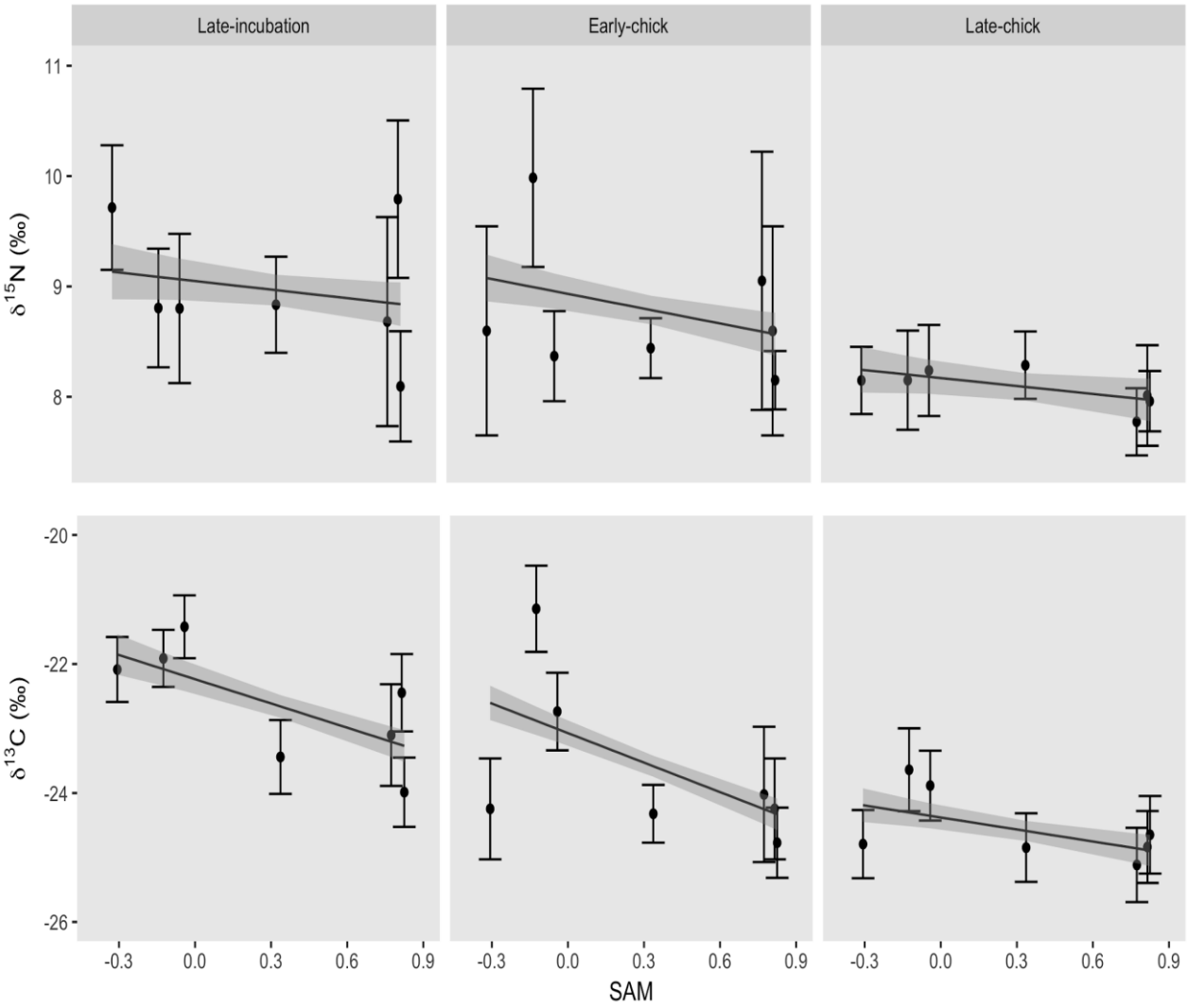


Figure 3.2. The influence of the SAM on $\delta^{15}N$ values (top panel) and $\delta^{13}C$ values (bottom panel), in the *Late-incubation*, *Early-chick* and *Late-chick* rearing stages. Mean $\delta^{15}N$ values are presented and grey shading indicates 95% prediction confidence intervals.

Inter-annual variability of breeding success

Breeding success varied considerably ($F_{11} = 23.51$, $P < 0.001$) during the 12 years of the study, with the lowest record in 2013 when only 22.0 ± 35.3% of eggs laid resulted in a chick compared to 75.3 ± 29.7% of eggs resulting in a chick in 2015 (Figure 3.3).

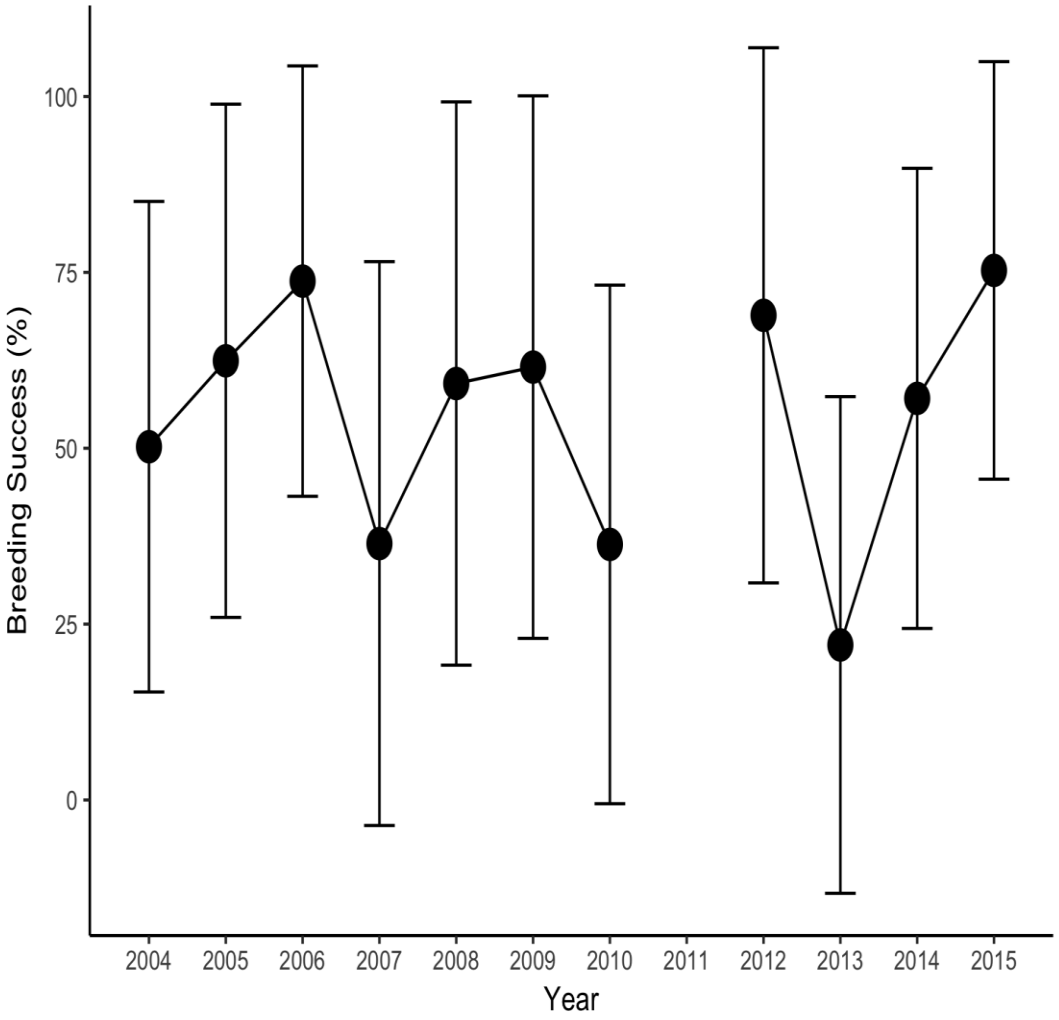


Figure 3.3. Annual breeding success (the proportion of chicks from eggs laid) of short-shearwaters at Wedge Island from 2004 - 2015 (excluding 2011) in 144 quadrats (1 - 21 burrows). Means ± SD are presented.

Discussion

Compound specific stable isotope analyses revealed that the trophic position of short-tailed shearwaters did not differ significantly between the breeding and non-breeding stages. Further, variability in bulk $\delta^{15}N$ values recorded during the breeding season was not attributed to prey trophic position but to latitudinal baseline variability across the broad ocean basin of the Southern Ocean. $\delta^{13}C$ correlated with the SAM suggesting that where short-tailed shearwaters foraged was influenced by environmental variability, but the trophic level of the prey they consumed was not affected.

Baseline variability of stable isotope values

Short-tailed shearwaters migrate rapidly between the Northern and Southern Hemispheres in as few as 13.5 ± 1.5 days, covering 840 ± 121 km a day (Carey et al., 2014). Considering this swift movement, it is unlikely that short-tailed shearwaters invest much time in foraging during the migration. Instead, the isotope values during the *Post-migration* stage in this study align closely with $\delta^{15}N$ and $\delta^{13}C$ values recorded during the non-breeding stage in the southeast Bering Sea (Baduini et al., 2006). Similarly, short-tailed shearwaters sampled upon their arrival into the North-Pacific Ocean following the breeding season had $\delta^{15}N$ values, which were indicative of Southern Ocean foraging (Gould et al., 2000, Minami et al., 1995). $\delta^{15}N_{Phe}$ was higher in the *Post-migration* stage and gradually tended towards zero through the breeding season. Hence the $\delta^{15}N$ values recorded in the *Post-migration* stage are carried-over from the non-breeding stage reflecting more enriched baseline concentrations of $\delta^{15}N$ in the North Pacific Ocean compared to the Southern Ocean (Kelly, 2000). These finding highlights that the differences in baseline $\delta^{15}N$ values are directly reflected in the bulk SIA values of short-tailed shearwaters, confirming that the source must be considered when making inferences about prey consumed by migratory and wide-ranging marine predators.

$\delta^{15}N$ and $\delta^{13}C$ values gradually became more depleted through the breeding season. Although we did not determine the foraging location of the birds in this study, the recorded gradual decline of isotopic values is probably associated with where the birds foraged. Previous studies have shown that short-tailed shearwaters predominantly forage north of the Antarctic Zone (AZ) during the *Post-migration* to *Late-Incubation* stages (Cleeland et al., 2014, Woehler et al., 2006) presumably because of low productivity and an extended sea ice zone

during spring (Smith et al., 2000, Arrigo et al., 2008). The core foraging area moves south to the AZ extending to the Antarctic Continental shelf by the *Late-chick* rearing stage (Cleeland et al., 2014). This shift in foraging location was apparent in the recorded $\delta^{13}C$ values in this study reflecting the pole-ward depletion of $\delta^{13}C$ in the Southern Ocean (Lourey et al., 2004, Goericke and Fry, 1994). Carbon isotope values have been correlated to foraging location in other species of Southern Ocean seabirds. For example, the $\delta^{13}C$ values of Adelie penguins (*Pygoscelis papua*) breeding at 67°S were more negative (-24.8 ± 0.5‰, $\delta^{13}C$) compared to northern rockhopper penguins (*Eudyptes moseleyi*) located in the subtropics 38°S (-19.5 ± 0.3‰, $\delta^{13}C$) (Cherel and Hobson, 2007). Further, Jaeger et al. (2010) estimated that wandering albatross (*Diomedea exulans*) returning with $\delta^{13}C$ values of ~ -22.9‰ correspond to foraging in the AZ and ~ -20.0‰ was representative of foraging within the Sub-Tropical Front (STF). Therefore, we estimate that birds returning from the Northern Hemisphere with $\delta^{13}C$ values of ~ -19‰ is indicative of near-shore foraging in the North Pacific Ocean (Baduini et al., 2006, Hunt et al., 1996); ~ -22‰ observed in the *Pre-laying* and *Incubation* stages corresponds to core foraging areas in the SAZ; and ~ -24‰ suggests foraging within the AZ during the chick rearing stages.

In the Southern Ocean $\delta^{15}N$ also tends closer to zero at higher latitudes (DiFiore et al., 2010, Wada et al., 1987). South of Australia $\delta^{15}N$ in surface waters is depleted by up to 1‰ in the AZ compared to the sub-Antarctic Zone (Lourey et al., 2003). This is thought to be a consequence of the remineralisation of sinking nitrate causing low nitrate surface waters (Sigman et al., 2000). The latitudinal depletion in $\delta^{15}N$ is apparent in deep-sea meiofauna (Veit-Kohler et al., 2013) and in blood plasma of wandering albatross (Jaeger et al., 2010). Further, $\delta^{15}N$ was enriched in Wilson's storm petrels (*Oceanites oceanicus*) when their core foraging areas were in the SAZ during the non-breeding season compared to when they predominantly foraged in the AZ during the breeding season (Quillfeldt et al., 2005). $\delta^{15}N$ of particulate nitrogen (PN) decreases by ~ 4‰ between September to March in the AZ but remains relatively stable in the SAZ (Lourey et al., 2003). In conjunction with more southerly foraging during the chick rearing stages, the seasonal depletion of $\delta^{15}N$ is bound to contribute to the low $\delta^{15}N$ values that were recorded during the *Late-chick* rearing stage.

Trophic position

We assumed that the assimilation of diet in short-tailed shearwaters would be similar to penguins. Therefore, to calculate the trophic position of short-tailed shearwaters from our AA-CSIA analyses, we used the TDF (3.6‰) determined for penguins by Lorrain et al. (2009) as these species also consume zooplankton and fish from the Southern Ocean. The trophic position of birds studied in the 2013 and 2014 breeding season ranged from 4 to 4.9 (4.6 ± 0.3), which is comparable to wild king penguin (*Aptenodytes patagonicus*) chicks (TP ~ 4.6) exclusively provisioned with myctophids (Lorrain et al., 2009). The enrichment of isotopes in the consumer is dependent on; the species size (Cabana and Rasmussen, 1996), the tissue used (Pinnegar and Polunin, 1999), species diet (McCutchan et al., 2003), and the water temperature the consumer lives in (Barnes et al., 2007). Considering that the king penguin chicks were only fed fish but short-tailed shearwaters eat zooplankton and myctophid fish (Connan et al., 2005, Cherel et al., 2005b), which are likely to occupy a lower TP than those consumed by a king penguin (Cherel et al., 2010), it was expected that the TP of short-tailed shearwaters would be substantially lower. This finding suggests species-specific trophic enrichment in these seabirds. Consequently, further study is warranted to provide a better estimate of trophic transfer between short-tailed shearwaters and their prey, if comparisons between species are to be made.

Even though adults select a wider diversity of prey, including low energy crab *Zoea spp.,* euphausiids and fish, during the non-breeding period (Ogi et al., 1980, Baduini et al., 2006, Hunt et al., 2002), our results and the findings from previous studies conducted during the breeding season suggest that adults consume a higher proportion of high-energy fish during the breeding season. For example, it was previously found that meals delivered to chicks of short-tailed shearwaters following a long-trip contained myctophids, primarily *K. anderssonni* (Weimerskirch and Cherel, 1998). This finding is consistent with other studies; fatty acid analysis and SIA indicated that the diet of short-tailed shearwaters was dominated by myctophid fish (Connan et al., 2010, Cherel et al., 2005b). Myctophids are an energy rich, abundant fish and are an important component of the diet of a range of marine predators in the Southern Ocean (Lea et al., 2002, Connan et al., 2007, de Bruyn et al., 2009, Reid et al., 2006, Collins et al., 2007). A diet high in fish may allow adults to meet increased energy demands when engaged in breeding activities.

Relationship between the SAM and isotope values

When the SAM was negative $\delta^{13}C$ was comparatively enriched and $\delta^{15}N$ values were slightly higher. $\delta^{13}C$ values were on average 1‰ higher when the SAM was negative, suggesting that adults foraged at lower latitudes, i.e. within the sub-Antarctic region. The modelled results indicated that nitrogen was influenced by the SAM. However, given that the estimated analytical error associated with measuring $\delta^{15}N$ values in this study was 0.3‰, coupled with the established declining latitudinal trend in nitrogen in the Southern Ocean (Lourey et al., 2004, Lourey et al., 2003), the differences in $\delta^{15}N$ values were most likely a result of sampling errors and short-tailed shearwaters foraging at lower latitudes when the SAM was negative.

The trophic position of adults during long-trips did not significantly vary among the seven years of this study. We also found that the lowest record of breeding success occurred during the 2013 breeding season at Wedge Island, yet compared to the 2014 breeding season, a year of average breeding success, the trophic level of their prey was not significantly different. This finding suggests that variable environmental conditions do not influence the trophic level of the prey short-tailed shearwaters consume when they are foraging for themselves.

During chick rearing, short-tailed shearwaters alternate between foraging locally to provide food to their chicks and undertaking long-trips to the AZ to replenish lost energy (Weimerskirch and Cherel, 1998, Einoder et al., 2011). The seesaw of ocean productivity between the mid to high latitudes of the Southern Ocean induced by the SAM is likely to influence the distribution and the abundance of prey in these regions (Thompson and Solomon, 2002, Marshall et al., 2004). The prevalence of positive SAM events in recent decades (Thompson and Solomon, 2002, Marshall et al., 2004), is likely to produce favourable conditions for short-tailed shearwaters' prey in the AZ but may result in prey depletion in areas surrounding the colony as the winds which promote upwelling are drawn pole-wards (Marshall, 2003). Certainly, we found that carbon values were more depleted when the SAM was positive, which suggests that birds foraged further from the colony when environmental conditions surrounding the colony would have been diminished.

The availability of prey surrounding the colony is likely to be a major factor influencing breeding success as this could influence the frequency of meals delivered to chicks, the quality

of prey and the size of meals. Local prey depletion may account for low breeding success at Wedge Island in some years, despite the adults' consistent trophic position throughout the study period. Certainly, the quality of prey fed to chicks can be important; common guillemots (*Uria aalge*) experienced wide spread breeding failure when chicks were fed a low-quality diet (Wanless et al., 2005). Indeed, lower quality prey and small meals resulted in reduced mass of short-tailed shearwater chicks in South Australia (Einoder et al., 2013). This suggests that the quality and abundance of prey surrounding Wedge Island is an important factor that influences breeding success.

This study shows that AA-CSIA can be used to differentiate between source and trophic $\delta^{15}N$ values of a wide-ranging seabird. This is important because wide-ranging marine predators consume prey in water masses with varying baseline levels of $\delta^{15}N$, which could lead to inaccurate estimates of their trophic position if these baseline values are not accounted for. This knowledge informed our study of the influence of the SAM on nitrogen and carbon values, suggesting that short-tailed shearwaters concentrate their foraging efforts in areas of greater productivity rather than eat greater abundances of lower trophic prey. The mechanisms underlying poor breeding success in some years bears further investigation. As we did not monitor the prey fed to chicks or the rate at which they were provisioned we cannot pinpoint the cause of the considerably low breeding success of 2013. Since adults do not vary their trophic position in response to climate fluctuations, it will be important to monitor the diet of chicks as this may explain the underlying causes for poor breeding performance. The combination of AA-CSIA and SIA opens a new way to study temporal change in the trophic position of wide-ranging seabirds, which is of increasing importance in a rapidly changing oceanic environment.

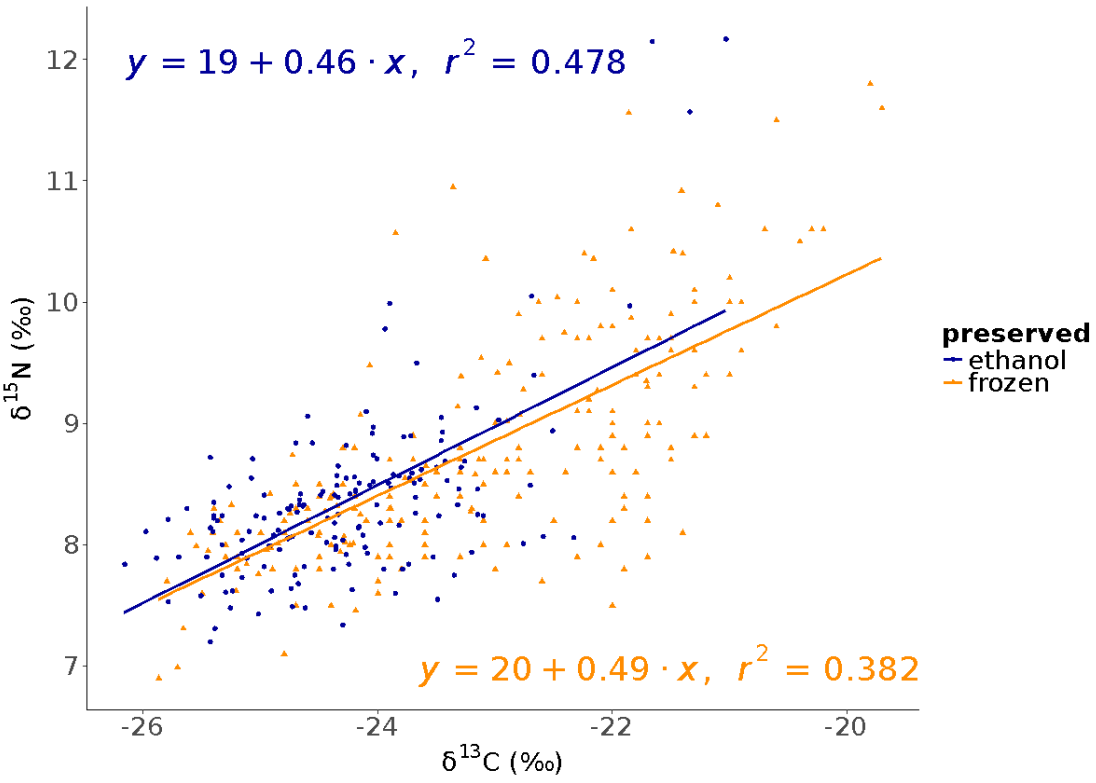
Acknowledgements

We thank the many volunteers and students who assisted with sample collection at Wedge Island. Logistic support getting to and from the island was provided by M. Porteous, D. Faloon and S.Talbot from the Institute for Marine and Antarctic Studies and A. Little from TASSAL. Funding to carry-out research was provided by the Winifred Violet Scott Charitable Trust, the Holsworth Wildlife Research Endowment, BirdLife Australia and the Australian Geographic Society.

Appendices

Appendix 3.1. Bulk $\delta^{15}N$ and $\delta^{13}C$ values (mean ± SD, range), from whole blood of short-tailed shearwaters at Wedge Island, 2004 - 2014. n = the total number of samples that were collected per stage within each breeding season. No repeat samples were collected from a bird in a stage within a breeding season.

Breeding Season	Stage	$\delta^{15}N$ (‰) mean ± SD (range)	$\delta^{13}C$ (‰) mean ± SD (range)	n
2004	Late-incubation	8.8 ± 0.5 (7.8 to 9.7)	-21.9 ± 0.4 (-22.8 to -21.2)	23
2004	Early-chick	10.0 ± 0.8 (8.8 to 11.8)	-21.1 ± 0.7 (-22.3 to -19.7)	25
2004	Late-chick	8.2 ± 0.4 (7.1 to 9.0)	-23.6 ± 0.6 (-24.8 to -22.0)	20
2005	Late-incubation	8.8 ± 0.7 (7.9 to 9.8)	-21.4 ± 0.5 (-22.1 to -20.6)	9
2005	Early-chick	8.4 ± 0.4 (7.5 to 9)	-22.7 ± 0.6 (-23.8 to -21.7)	19
2005	Late-chick	8.2 ± 0.4 (7.5 to 8.9)	-23.9 ± 0.5 (-24.7 to -23.1)	21
2006	Late-incubation	9.7 ± 0.6 (8.7 to 10.8)	-22.1 ± 0.5 (-22.9 to -21.1)	14
2006	Early-chick	8.6± 0.9 (6.9 to 11.0)	-24.2 ± 0.8 (-25.9 to -23.1)	22
2006	Late-chick	8.1 ± 0.3 (7.6 to 8.8)	-24.8 ± 0.5 (-25.8 to -23.6)	25
2007	Late-incubation	9.8 ± 0.7 (8.7 to 11.6)	-22.4 ± 0.6 (-23.3 to -21.4)	21
2007	Early-chick	8.6 ±0.9 (6.9 to 11.0)	-24.2 ± 0.8 (-25.9 to -23.1)	22
2007	Late-chick	8.0 ± 0.5 (7 to 9.1)	-24.8 ± 0.6 (-25.7 to -24.2)	20
2012	Post-migration	12.3 ± 1.3 (8.1 to 14.1)	-19.8 ± 1.2 (-24.4 to -18.8)	18
2012	Early-incubation	9.3 ± 0.7 (8.3 to 10.6)	-21.9 ± 0.9 (-23.2 to -20.3)	14
2012	Late-incubation	8.7 ± 0.9 (8.0 to 12.2)	-23.1 ± 0.8 (-24.4 to -21.0)	17
2012	Early-chick	9.1 ± 1.2 (7.9 to 12.2)	-24.0 ± 1.0 (-25.1 to -21.3)	19
2012	Late-chick	7.8 ± 0.3 (7.2 to 8.3)	-25.1 ± 0.6 (-26.2 to -23.7)	20
2013	Post-migration	13.0 ± 1.6 (8.4 to 15.0)	-20.3 ± 1.0 (-23.0 to -19.3)	18
2013	Pre-laying	8.9 ± 0.9 (7.8 to 11.2)	-22.4 ± 1.3 (-24.8 to -19.3)	14
2013	Early-incubation	8.3 ± 0.7 (7.5 to 10.4)	-22.7 ± 0.7 (-23.7 to -21.4)	21
2013	Late-incubation	8.1 ± 0.5 (7.3 to 9.5)	-24.0 ± 0.5 (-25.2 to -23.2)	19
2013	Early-chick	8.2 ± 0.3 (7.6 to 8.7)	-24.8 ± 0.5 (-25.6 to -23.8)	18
2013	Late-chick	7.8 ± 0.3 (7.3 to 8.4)	-24.6 ± 0.6 (-25.7 to -23.4)	16
2014	Post-migration	13.3 ± 1.0 (11.9 to 15.6)	-18.9 ± 0.7 (-21.0 to -18.2)	20
2014	Pre-laying	9.6 ± 0.7 (8.2 to 10.6)	-21.7 ± 0.7 (-23.7 to -20.4)	20
2014	Early-incubation	9.0 ± 0.4 (8.4 to 9.0)	-22.4 ± 0.3 (-22.9 to -21.9)	20
2014	Late-incubation	8.8 ± 0.4 (8.3 to 10.0)	-23.4 ± 0.6 (-24.1 to -21.9)	16
2014	Early-chick	8.4 ± 0.3 (7.9 to 8.8)	-24.3 ± 0.4 (-25.1 to -23.7)	14
2014	Late-chick	8.3 ± 0.3 (7.5 to 9.0)	-24.8 ± 0.6 (-25.8 to -24.0)	20
Total				545

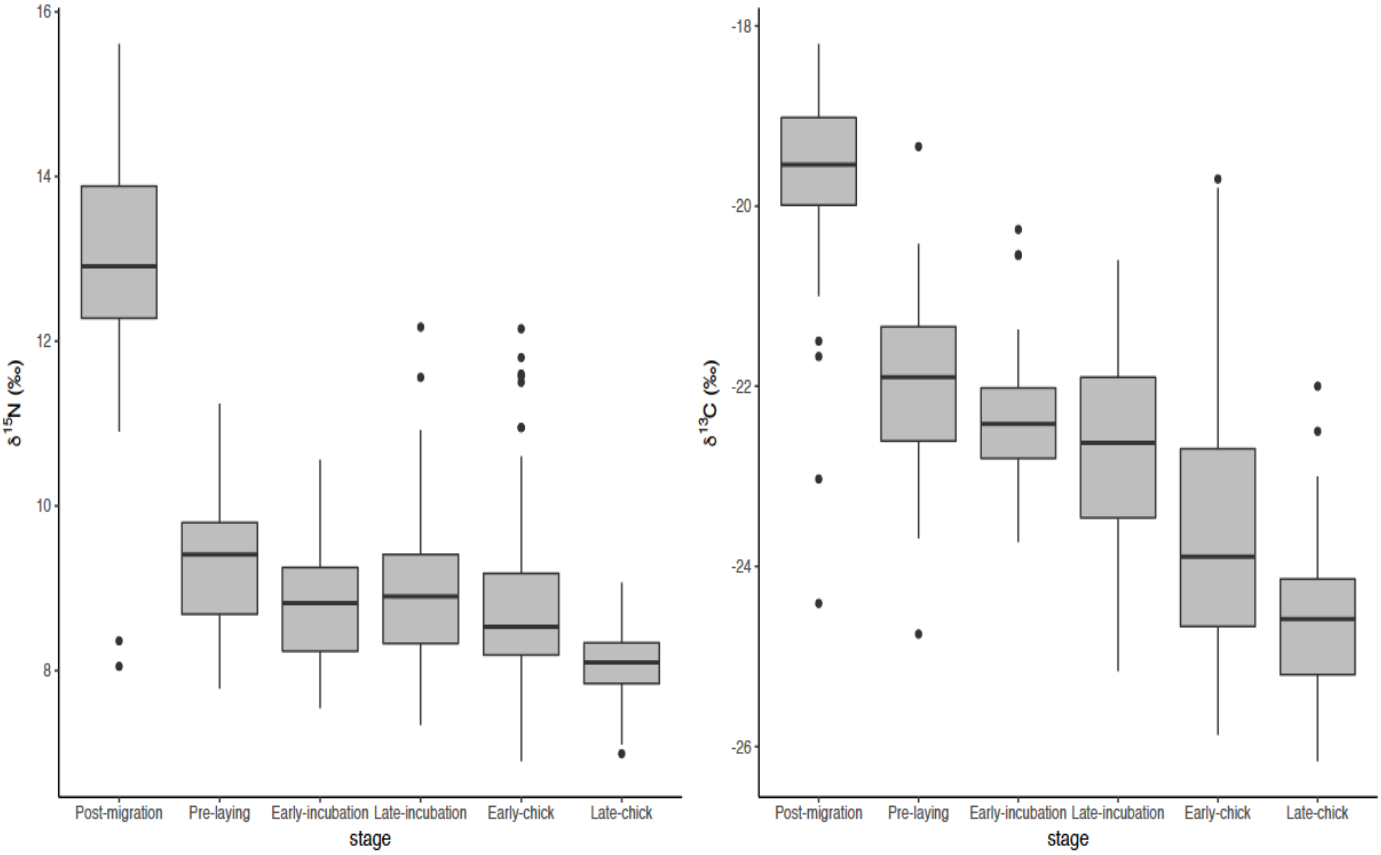


Appendix 3.2. The effect of preservation of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) of short-tailed shearwater blood samples in either ethanol (blue) or by freezing (orange).

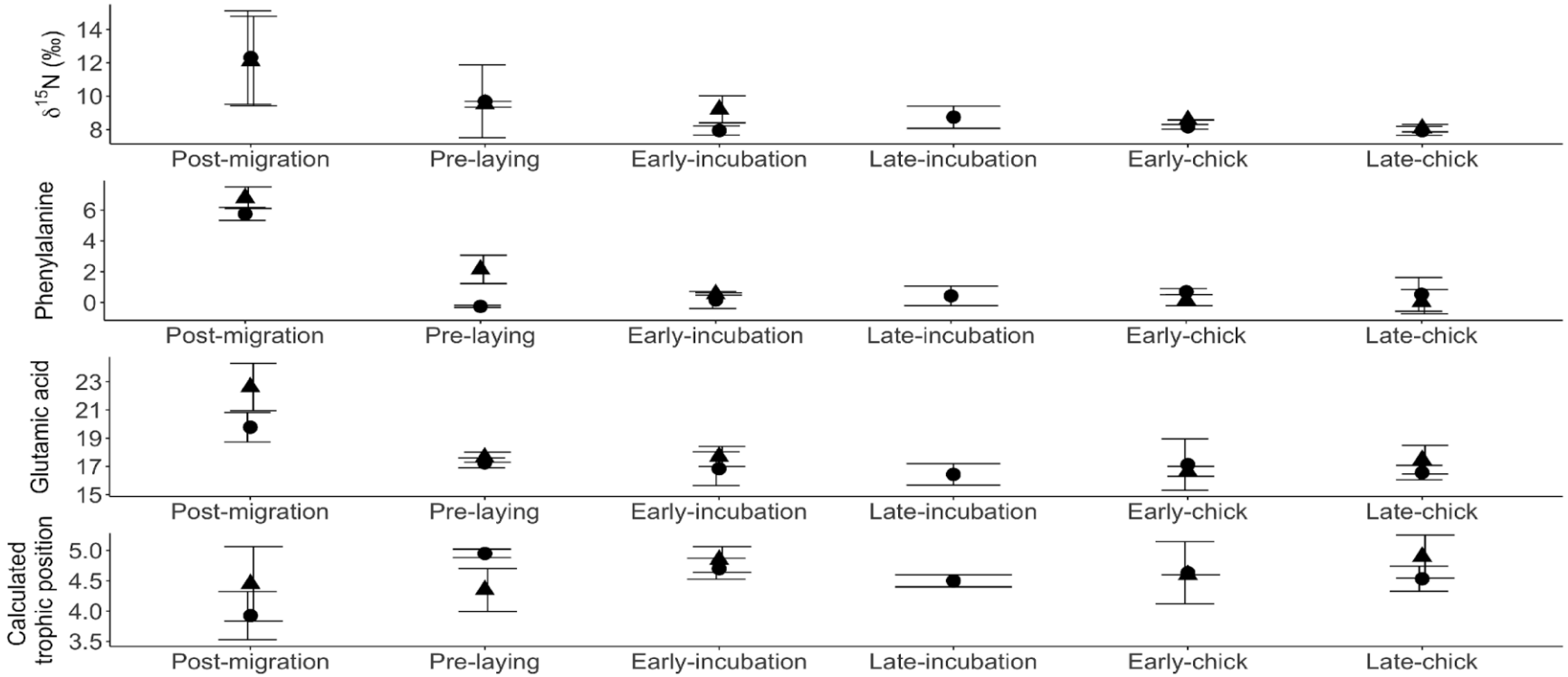
Appendix 3.3. AA-CSIA laboratory methods

Dried whole blood (60 - 80 mg, dry wt.) was hydrolysed with one mL of 6 M HCl at 150°C for 70 min and then evaporated to dryness under a stream of N_2 at 60°C. Samples were re-dissolved in 0.01 M HCl and amino acids purified using GracePure ™ SPE Cation-X cartridges with amino acids eluted with 4 mL 2 M NH_4OH. Samples were evaporated to dryness under a stream of N_2 at 60°C and derivatives suitable for gas chromatography obtained by esterifying the carboxyl group by addition of 1 mL of acetyl chloride in isopropanol (1:4) and heating to 110°C for 1 hr. Samples were again evaporated to dryness under a stream of N_2 at 60°C and trifluoroacetylation of the amino group achieved with the addition of 200 µL trifluoroacetic anhydride and 800 µL CH_2Cl_2 and heated to 100°C for 15 min. Samples were evaporated to dryness under a stream of N_2 at 60°C and further purified by re-dissolving in 1 mL of hexane / dichloromethane (4:1) and 1 mL of aqueous phosphate buffer (pH 7.0, 5.36 g K_2HPO_4 and 2.62 g KH_2PO_4 in 500 mL of milli Q H_2O). Samples were vortex mixed for 1 minute, centrifuged at 2000 rpm for 2 minutes and the hexane layer containing the amino acids collected. This purification step was repeated twice more, the combined hexane layers evaporated to dryness under a stream of N_2 at 60°C and re-dissolved in ethyl acetate for analysis.

The $\delta^{15}N$ isotope values of individual amino acids were determined with a Trace GC gas chromatograph interfaced with a Delta V Plus isotope ratio mass spectrometer (IRMS) through a GC-C combustion furnace (980°C), reduction furnace (650°C) and liquid N_2 cold trap. The samples (0.5 µL) were injected splitless (split/splitless injector, 10:1 split ratio) onto a forte BPX5 capillary column (30 m × 0.32 mm × 1.0 µm film thickness) at an injector temperature of 180°C with a constant helium flow rate of 1.5 mL min^{-1}. The column was initially held at 50°C for 2 min and then increased to 120°C at a rate of 10°C min^{-1}. Once at 120°C, the temperature was increased at a rate of 4°C min^{-1} to 195°C and then at 5°C min^{-1} to 235°C where it was held for 5 min. The temperature was then further increased to 300°C at 15°C min^{-1} and held for 8 min.



Appendix 3.4. Mean $\delta^{15}N$ and $\delta^{13}C$ values for the *Post-migration*, *Pre-laying*, *Early-incubation*, *Late-incubation*, *Early-chick* and *Late-chick* rearing stages. Samples were only collected in the *Post-migration* to *Early-incubation* stages during 2012 - 2014. Samples were collected across the entire study period during the *Late-incubation* to *Late-chick* rearing stages (2004 - 2008 and 2012 - 2014).



Appendix 3.5. $\delta^{15}N$ (mean ± SD), AA-CSIA of phenylalanine, glutamic acid and calculated trophic position of short-tailed shearwaters (n = 32) from Wedge Island in each stage of the breeding season. 2013 values are depicted by circles, 2014 values are depicted by triangles. Samples were not available for the *Late-incubation* stage in 2013.

CHAPTER 4 THE SOUTHERN ANNULAR MODE INFLUENCES FORAGING BEHAVIOUR AND CHICK FLEDGING MASS OF A SOUTHERN OCEAN PREDATOR, THE SHORT-TAILED SHEARWATER

Abstract

Climate induced perturbations in the marine environment can cascade through entire ecosystems. Such variability can be linked to large-scale climate indices and is known to affect wide ranging marine animals across their ranges. Given that the Southern Annular Mode (SAM) is coupled with ocean productivity in the Southern Ocean, we assessed whether this index could be used to better understand the link between foraging behaviour and breeding performance of short-tailed shearwaters *(Ardenna tenuirostris*). Adult birds were equipped with global location sensing devices (GLS) during the 2010 to 2015 breeding seasons to quantify the effect the SAM had on the distance birds travelled to their core foraging areas and their foraging activity throughout the breeding season. There was a negative relationship between both the distance birds flew to their core foraging areas and foraging activity in the *Pre-laying* and *Late-chick rearing* stages when the SAM was negative. We also used the SAM and the Pacific Decadal Oscillation (PDO), and also local measures of ocean productivity (sea surface temperature and chlorophyll *a*) in the areas birds used during chick provisioning, to determine if climate variability explained breeding participation, breeding success and fledging weight. Chick mass was lower when local SST was above average and when the SAM was positive. However, the number of birds that engaged in breeding activities and breeding success were not related to climate variability, suggesting that the inter-annual fluctuations in the number of birds breeding and breeding success may be related to top-down factors, such as onshore predators.

Introduction

Animals must successfully locate food to ensure that they acquire enough energy to raise offspring and maintain other basic life processes. This is especially challenging when prey are unevenly distributed across wide areas, such as large ocean basins. In marine systems, climate variability, including sea surface temperature (SST), wind strength, mixing of the water column and solar radiation, are linked to primary production, which, through bottom-up processes, supports predators and their prey (Behrenfeld et al., 2006, Field et al., 1998). Ecologists often use large-scale climate indices to help unravel the complex interactions between the foraging distribution and reproductive success of wildlife (Ainley and Hyrenbach, 2010, Seyboth et al., 2016). Such indices deliver a time-integrated measure of atmospheric air

pressure and circulation patterns, which influence ocean productivity over vast distances (Forchhammer and Post, 2004, Stenseth et al., 2003).

In the Southern Hemisphere, the Southern Annular Mode (SAM) is a large-scale climate index that defines the atmospheric pressure between the middle and high latitudes of the Southern Ocean and it is known to influence primary productivity (Lovenduski and Gruber, 2005, Thompson et al., 2000). The positive phase of the SAM is strongly associated with the southward contraction of the westerly wind belt to the Antarctic Zone (AZ) (~65ºS) (Ho et al., 2012). SST also decreases between the AZ and the Polar Frontal Zone (PFZ), and iron supply increases due to wind-driven upwelling leading to increased primary production in the AZ (Lovenduski and Gruber, 2005). Further, when the SAM is positive, increased winds and cooler SST results in greater sea ice concentration (Massom and Stammerjohn, 2010), which can also affect Southern Ocean primary production (Lovenduski and Gruber, 2005, Simpkins et al., 2012). Conversely, down-welling is initiated in the mid-latitude zones north of 45ºS with only a weak cooling of SST (Hall and Visbeck, 2002, Lefebvre et al., 2004). Through these mechanisms, the SAM has been found to influence krill abundance (Fielding et al., 2014), the timing of royal penguin (*Eudyptes schlegeli*) breeding (Hindell et al., 2012), and the reproductive rates and survival of Southern Ocean seabirds and seals (Descamps et al., 2016, Forcada and Hoffman, 2014, van den Hoff et al., 2014).

The SAM is predicted to be increasingly positive into the future (Marshall et al., 2004, Thompson and Solomon, 2002), this could influence breeding participation and success and potentially the long-term population viability of many Southern Ocean predators. The amount of energy a marine predator has in reserve can influence whether it breeds in a particular year (Boyd, 2000). Therefore, insufficient prey availability prior to breeding can result in delays in the onset of breeding (Afan et al., 2015) or abandonment of the attempt (Ancona et al., 2011). For central place foragers, such as breeding seabirds, the heterogeneous distribution of their prey, the cost of finding and transporting food and the energetic requirements of raising chicks, means that individuals must balance locating and procuring food for their young and ensuring their own long-term survival (Benoit-Bird et al., 2013, Boersma and Rebstock, 2009). Although, seabirds can compensate for low prey abundance and distribution by travelling further (Montevecchi et al., 2009) the resulting increased trip duration can reduce chick

growth and survival if the chick receives fewer calories (Boersma and Rebstock, 2009, Yamamoto et al., 2011).

The short-tailed shearwater *(Ardenna tenuirostris)* is an abundant wide ranging predator of the Southern Ocean during the austral summer (Woehler et al., 2006) and also of the North Pacific Ocean where it spends the non-breeding season (Yamamoto et al., 2015). Thus, short-tailed shearwaters are likely to respond to climate processes, which operate at large scales. The abundance and distribution of prey in the North Pacific is likely to influence the birds' mass on its return to the colony and subsequently their propensity to breed. The Pacific Decadal Oscillation (PDO) is a monthly index of climate > 20°N of the North Pacific Basin (Mantua et al., 1997). Positive values correspond to anomalously warm SST and negative values indicate anomalously cold conditions (Mantua and Hare, 2002). This broad-scale climate index has been found to influence the availability of prey of some seabird species (Vandenbosch, 2000, Watanuki and Ito, 2012), therefore the PDO could influence the number of short-tailed shearwaters that engage in breeding activities after their return to the Southern Hemisphere.

During the breeding season, short-tailed shearwaters forage bi-modally as they rely on local resources near the colony to provision their chick but undertake long-trips to the Antarctic for self-maintenance (Weimerskirch and Cherel, 1998). Therefore, local measures of ocean productivity, such as SST or wind surrounding the colony, may be indicators of prey availability influencing chick condition and survival, as the adults are reliant on local prey to provision the chick (Berlincourt and Arnould, 2015, Einoder et al., 2013). However, when adults range widely during long-foraging trips, they may modify their foraging strategies dependent on the breeding stage (and therefore the requirements at the nest) and the SAM. Our study had the following aims: 1) ascertain the seasonal distribution of breeding birds during long-trips, 2) determine whether the SAM influences the distance birds travel to reach core foraging habitats, 3) assess whether foraging activity varied between breeding stages and if it was influenced by the SAM, 4) determine the foraging range of short-tailed shearwaters during local chick provisioning trips, and 5) measure the influence of the PDO, the SAM and local SST and chlorophyll *a* (Chl a) concentrations on breeding participation and output.

Methods

Ethics statement

All animal handling and instrumentation was carried-out under Research Permits (DPIPWE: FA10212, FA13009, FA14063, FA15083, FA16077) and University of Tasmania Ethics Committee permits (A11338, A128942, A15572).

Study site and species breeding biology

This study was conducted at Wedge Island (43° 07' S, 147° 40' E). Wedge Island is at the southern extent of the species' breeding range and supports a colony of 20,000 - 25,000 breeding pairs. The short-tailed shearwater is a medium sized Procellariiforme that breeds in southern Australia, during the Austral summer (October - April) and migrates to the Northern Hemisphere for the non-breeding season (April - October) (Marshall and Serventy, 1956). Breeding is highly synchronous with birds returning in October. A single egg is laid between the last week of November and the first week of December. Incubation lasts, on average, 53 days and chick provisioning ends by the middle of April when the adults leave for the non-breeding migration. At this time the chicks are left to finish their development without further provisions (Serventy and Curry, 1984). During chick rearing, adults alternate between short local foraging trips (1-3 days) to provision the chick and long-trips (7-32 days) to replenish the adults' condition (Einoder et al., 2011, Weimerskirch and Cherel, 1998). The breeding season has four stages: 1) *Pre-laying* (October 25 - November 20), (2) *Incubation* (November 20 - January 20), (3) the *Early-chick rearing* stage (January 21 - February 28), and (4) the *Late-chick rearing* stage (March 1 - March 31). The breeding season is referred to as the start year of the breeding season.

Global location sensors (GLS)

To quantify long trip foraging parameters, global location sensing devices (GLS) were deployed between 2010 and 2014. MK-19 GLS tags (British Antarctic Survey, Cambridge, UK; 16x14x6 mm, 2.5 g) were used in 2010 and 2011, MK-3005 GLS tags (Biotrack Ltd., Wareham, UK; 2.5 g) in were deployed in 2012 and 2013 and Intigeo ®C250 GLS tags

(Migrate Tech Ltd, Cambridge, UK; 18X15X6 mm, 3 g) were used in 2014 (Table 4.1). GLS tags sampled ambient light level every minute and recorded the maximum light every five minutes, which was used to estimate the birds' location (Hill, 1994). Sea surface temperature was recorded when the device was continuously wet for 20 minutes (with a resolution of -0.125°C, ± 0.5°C accuracy). Minimum, maximum and mean temperatures were sampled every four hours, allowing the data to be compared to remotely sensed SST (C250 tags). The MK19 and MK3005 tags provided temperature data when devices were submerged for 25 minutes, stopping when the sensor was dry for six seconds or longer. All loggers recorded when the device was either wet or dry which was used to indicate foraging activity; (i) either foraging or resting on the surface (wet) or (ii) flying (continuously for over 25 minutes) or attending the burrow (dry). The MK19 and MK3005 tags recorded activity data (number of seconds wet/dry) on state change (within three seconds), if the state persisted for longer than six seconds. The C250 tags recorded the state (either wet or dry) and the number of seconds since a change in state, providing the amount of time the bird was either in flight or in or on the water.

Tags were attached to the tarsus following Cleeland et al. (2014). The total weight of the tag and attachment was 4 - 4.5 g. Tags were calibrated at the deployment site by placing them under the open sky for 2 to 7 days prior to deployment (Lisovski et al., 2012). A total of 192 birds were instrumented with tags which were deployed either prior to the *Pre-laying* exodus in October (when the breeding status was unknown), or onto breeding birds during the *Incubation* and chick-rearing stages or at the end of the breeding season (Appendix 2.1). Devices were retrieved throughout the breeding season or during subsequent breeding seasons (n = 145). All birds were recaptured at the colony, either in their burrows or on the surface near their burrows, except for one bird, which was found dead in South Australia in November 2013 (cause of death unknown). Overall, tags were deployed for 1 to 52 months (mean ~8 months). Ten birds were recaptured 18 months to 52 months after deployment. Of these, tags fell off four birds prior to recapture and one device failed eight months after deployment, resulting in data from six birds tracked for two seasons. Overall, five loggers failed shortly after deployment and in addition a subset of tags only provided data for a portion of the time they were deployed; thirty Biotrack Ltd, and three Migrate Tech Ltd tags failed one week to three months and one to six months after deployment respectively. Further to this, four recovered tags had a large proportion of suspect twilight data and could not be used in

analyses. In total 99 tags provided data that were used in analyses. To check for device effects, the success of a subset of the burrows used for breeding at Wedge Island (2010 = 185, 2012 = 163, 2013 = 126, 2014 = 226) were compared to the breeding success of birds used for tracking. Due to logistical constraints it was not possible to determine the breeding success of birds on which devices were deployed during the 2011 breeding season.

Table 4.1. The year, the model, and the number of GLS loggers deployed and retrieved, from short-tailed shearwaters tracked at Wedge Island, and the number of tracks included in analyses in each of the *Pre-Laying*, *Incubation*, *Early-chick* and *Late-chick* stages.

				Tracks and activity data used in analyses per stage [a]**			
Year	**Model**	**GLS deployed***	**GLS Recovered**	**Pre-laying**	**Incubation**	**Early-chick**	**Late-chick**
2010	MK19	50	35	14 (14)	13 (13)	13 (13)	2 (2)
2011	MK19	22	16	2 (0)	15 (12)	14 (13)	14 (13)
2012	MK3005	37	21	18 (8)	11 (8)	8 (1)	5 (3)
2013	MK3005	40	36	9 (4)	15 (10)	11 (7)	7 (7)
2014	C250 & MK3005	45	36	5 (1)	18 (11)	16 (11)	20 (20)
Total	**-**	**194**	**144**	**48 (27)**	**72 (54)**	**62 (45)**	**48 (45)**

(a) The number of birds tracked, and activity data displayed in parentheses that could be used for analyses to compare foraging parameters between stages where data was available for at least 50 % of a given stage.
(b) The tags used in this study had limited capacity to store activity data (~ 7 months). In the instances where the logger had been deployed for longer than 7 months, the tag ceased recording activity data, which meant that some individuals did not have activity data available for some of the stages of which it was tracked. Individual bird activity data were only included if it were available for ~50% of a breeding stage.
*Excluding birds only tracked for the non-breeding period

**Excluding non-breeders and failed breeders

Location estimation

Daily positions were estimated from the raw light and sea surface temperature (SST) values in the R package *SGAT* (Sumner et al., 2009, Wotherspoon et al., 2013). This package uses the Threshold method (Hill, 1994), where location estimates are computed using the solar zenith angle calculated during the calibration period. Because the tags deployed on these birds were attached to their leg the sensor can sometimes be shaded by the bird when it is in flight or when it is sitting on the surface at the colony. Such shading can considerably affect the estimation of latitude positions. Therefore, where shading of the tag's sensor prevented accurate estimation of the twilight curve, individual twilights were manually adjusted to match the overall trend in the light level prior to twilight, based on the set light threshold identified during the pre-processing stage. Further, sometimes when a bird is sitting on the surface at the colony or when nesting; wet/and or muddy and sufficiently salty feathers can result in false SST readings. These readings are typically anomalously higher than the median SST temperature, and so this data was identified and removed using the SSTfilter and selectData functions in `SGAT`.

SGAT is based on a Bayesian framework that uses Markov Chain Monte Carlo (MCMC) to estimate the posterior distribution of locations (Sumner et al., 2009). Each birds' locations were estimated (and 95% CI) using a set of priors that included: 1) a spatial probability mask, to exclude locations on land; 2) a movement model where the average speed of travel between successive locations was assumed to be Gamma distributed, thus the probability of distribution of speeds is estimated using the mean time intervals between twilights (in hours), limiting the distance between locations; and, 3) to improve accuracy of location data, SST was used to constrain the location estimation. The final estimated track was calculated using a Metropolis algorithm to burn in 12 000 iterations. The posterior distribution of the filtered mean temperature data recorded by the device was compared to remote satellite derived SST data, obtained from the Earth System Research Laboratory http://www.esrl.noaa.gov/psd/repository/entry/show?entryid=12159560-ab82-48a1-b3e4-88ace20475cd); and, 4) to account for twilight errors associated with tag shading, a log-normal probability distribution was applied to twilights, providing more accurate location estimation (Wotherspoon et al., 2013).

Long-trip foraging parameters

Given the uncertainty of location estimates from GLS tags (202 ± 117 km) (Phillips et al., 2004), and because latitudes cannot be accurately estimated during the equinox, individual trip start and end times could not be identified from the location data after the incubation stage. Typically birds only spent between 7 to 9 hours at the colony at night during the chick rearing stages. This is likely to be an equivalent period of time which birds spent, in continuous flight, when they were returning from the Antarctic region. So, activity data could not be used to determine the start and end of trips because it was not possible to differentiate between time spent at the colony compared to time in transit. Subsequently, all locations estimates within 200 km of the colony were excluded from analyses so as to remove any twilight readings recorded when the birds were at the colony or when birds were undertaking a short trip in waters surrounding the colony. Therefore, individual trips were not used in analyses: rather 1) each individual's core foraging area for each stage of the breeding stage was estimated, 2) the core foraging area was defined as the 90^{th} percentile of the kernel density of the complete set of posterior location estimates for that bird and stage, and 3) the mean distance from the colony to the core area was calculated and this was the response variable in the subsequent analyses. Where a bird was not tracked for at least 50 percent of a stage, it was excluded from analyses for that stage. We set a minimum threshold of 50 percent, because this provided ~15.5 days of data, providing a minimum of 1-3 long-trips per bird per stage (Cleeland et al., 2014). Except for the pre-breeding exodus, non-breeding birds were also excluded from analyses.

Foraging activity

Short-tailed shearwaters can forage during periods of darkness (Berlincourt et al., 2015). However, the birds in this study spent more time at the surface during periods of darkness ($t = -7.9$, $df = 12341$, $p < 0.0001$), which was most likely associated with time spent resting and rafting in waters surrounding the colony (Phalan et al., 2007, Shaffer et al., 2009, Wilson et al., 2009). Consequently, we excluded night activity data, as it was not possible to differentiate between periods of rafting or foraging. To compare at-sea activity (time spent in or on the water) between stages, the daily total wet time (*pwet*) was calculated for each bird and the data was combined with the corresponding location estimates to determine the proportion of wet

activity data by foraging location. Although it is likely that a proportion of the time spent on the water's surface during daylight hours would be associated with resting rather than foraging, the amount of time a logger is wet is considered to provide an acceptable indication of seabird foraging activity (Catry et al., 2009, Krietsch et al., 2017). As with the location data, only breeding birds that were tracked for at least 50 percent of a stage were included in analyses.

Short foraging trips: animal capture and handling

To quantify fine-scale movements of short-tailed shearwaters during chick provisioning trips (short-trips), adults were captured in their burrow, banded, weighed, and were equipped with a Global Positioning System (GPS) recorder (details below). Ten birds were equipped in February to March 2014, and 14 birds in January to March 2015 (> 1 day in duration).

Device attachment

Two types of GPS loggers were deployed, CatTraQ GPS logger (GM, SC 29622, USA), and Gypsy-4SB, (35 x 19 x 4 mm, 5.5 g, Technosmart, Rome, Italy) powered by a 350 mAh battery (20 x 30 x 4 mm, 5.2 g). The loggers were waterproofed using glue lined heat shrink tubing. To attach the GPS logger, three pieces of Tesa tape (Tesa, Hamburg, Germany) were wrapped around the device and several feathers on the central lower back. The archival GPS loggers recorded the birds' position every 5 minutes and every 3 minutes (± 5 - 10 m) in 2014 and 2015 deployments respectively. The CatTraQ GPS unit and packaging weighed approximately 25 g and the Gypsy-4SB GPS unit weighed approximately 16 g in air, equating to less than 3% of the body weight of the average short-tailed shearwater on Wedge Island (590 ± 64.4 g, n = 280).

Trip duration (hr), total distance travelled (km), maximum distance from the colony (km), bearing from the most distal position from the colony (°) and mean and maximum horizontal speed (km/h^{-1}) were calculated. Due to the small number of trips recorded in 2014 (n=3), trip characteristics could not be compared between years and consequently, all data were pooled.

Census

The number of birds breeding in the colony were estimated from 2004 to 2015. Quadrats (2 m diameter) were permanently laid out in transects to represent the different vegetation communities and the varying density of short-tailed shearwater burrows across the island. The content of each burrow within a quadrat was checked in December, following the laying period, with a custom made burrow camera to ascertain whether a bird and an egg were present. For further details on the survey methods please refer to Vertigan et al. (2012). To determine breeding success, burrows that contained an egg were inspected again in April, prior to chick fledging. Breeding success was defined as the proportion of chicks that were successfully raised from the number of eggs laid. Logistical constraints prevented the chick census being carried-out in April 2012; hence breeding success data were not available for the 2011 breeding season. Due to the friable nature of the substrate in some sections of colony, it was not always possible to survey all quadrats each year. Removal of these quadrats resulted in 144 quadrats that were surveyed in each year. To determine chick condition prior to fledging (70 - 80 days after hatching), a subset of chicks were weighed two to three weeks prior to fledging in 2005 (n = 26), 2006 (n = 40), 2007 (n = 17), 2008 (n = 18), 2013 (n = 54), 2014 (n = 61), 2015 (n = 110), 2016 (n = 50). Chicks were removed from burrows and weighed in a cloth bag using a 1 or 2 kg Salter spring balance (Super Samson models, Salter Australia Pty Ltd, Melbourne, Australia).

Environmental data

To assess the relationship between distance to core foraging areas during long-trips and environmental variability, we compared travel distance and the SAM (https://legacy.bas.ac.uk/met/gjma/sam.html) (Marshall, 2003). To provide an index of prey availability during short-trips, daily SST records were extracted from the area that short-tailed shearwaters utilised when provisioning their chicks (146 - 148°E, 42° - 43°S) from http://mur.jpl.nasa.gov. Chlorophyll *a* (Chl *a*) data were extracted for the same region using the NOAA ERDAAP database at https://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html?page=1&itemsPerPage=1000. As the condition of birds upon their return to the colony following the winter migration is likely to influence participation in subsequent breeding activities, we used the PDO index (May –

September) available at www.jisao.washington.edu/pdo as an index of the availability of prey in the North Pacific foraging areas. To determine whether the SAM affected the number of birds that bred, the local SST and SAM data were averaged from April to November, as the conditions in the Southern Ocean prior to breeding are also likely to influence breeding participation. To compare the stage-specific effects of environmental variability and foraging behaviour during the breeding season, we used the SAM data averaged from October to April (i.e. the breeding season), for each year of the study. To examine the influence of environmental conditions on breeding success, we expected that local summer SST, Chl *a* and the SAM conditions (December to March) would affect breeding success and chick fledging mass.

Statistical analysis

To determine whether the SAM influenced the within-breeding season variability in distance to core foraging areas during long foraging trips, we constructed an *a priori* Linear Mixed Effects model (LME). The model included two terms (SAM and stage) with plausible interaction terms of breeding stage, distance to core foraging areas in addition to a global model, which included all interactive terms. The models were developed using the R package `lme4` (Bates et al., 2015). We used a corrected Conditional Akaike's Information Criteria (cAIC) to elect the best model using the R package `cAIC4` (Saefken et al., 2014). To assess whether foraging activity (the proportion of time wet; *pwet*) was influenced by the SAM, we used a LME model that also included SAM and stage, and to account for temporal autocorrelation of the daily activity data, we used an autoregressive correlation (AR(1)) structure. Foraging activity was logit transformed to obtain approximately normal distributions. All models incorporated bird ID as the random term and a Gaussian family distribution, and the model fit was estimated using maximum likelihood. Because the `LMER` package does not handle auto-correlated data, the best model was selected using Akaike's Information Criteria (AIC) (Burnham and Anderson, 2002) and Akaike's weight, using the small sample size correction (AIC_C). The most parsimonious model was selected as the simplest model of those where $\Delta AICc \leq 2$.

The proportion of birds which bred and breeding success, data were tested for Gaussian distribution using a Shapiro-Wilks test and data were not found to depart from normal

distributions (Appendix 4.1). One-way ANOVAs were used to determine the inter-year variability in the proportion of adults that engaged in breeding and also breeding success. To assess whether breeding effort (number of birds engaged in breeding activities) and breeding success was related to environmental conditions we used linear models. The assess if there was a relationship between the environmental conditions birds experienced during the non-breeding stage (and therefore influenced their condition upon arrival to the breeding colony) we included the PDO as a predictor variable. Further, because it is plausible that the environmental conditions prior to the breeding season in the Southern Ocean could carry-over to the breeding period and subsequently influence the numbers of birds which commence breeding, the SAM, local SST and Chl *a* were also included as predictor variables. The resulting models were fitted and ranked using AIC_c for small sample sizes, and Akaike's weights. To assess whether breeding success (response variable) was related to Austral summer conditions, the SAM, local SST and local Chl *a*, were included as predictor variables in linear models and these were also fitted and ranked using AIC_c for small sample sizes, and Akaike's weights. Data are presented as means plus or minus standard deviation (SD), unless stated otherwise, *t*-Tests are two tailed and tests were considered significant at $p < 0.05$.

Results

Long-trip foraging parameters

During 2010 to 2015, we recovered 144 GLS tags (Table 4.1, Appendix 2.1). Carrying a GLS device did not significantly affect breeding success; breeding success of tracked birds (mean 58.9 ± 16.7 %) was comparable to control birds (mean 46 ± 21 %) (t = -0.95756, df = 6, P = 0.377). During the breeding season, the core foraging areas extended from regions just north of the colony within the Subtropical Zone (STZ), to areas associated with the Sub-Antarctic Polar Front (SAF) and Antarctic Polar Fronts (APF), to as far south as the ice edge (69°S) and ranged from 90°E to 170°E (Figure 4.1). There was considerable variation in the distance birds travelled from Wedge Island, among the breeding stages (ANOVA: $F_{3,227}$ = 29.7, P < 0.0001). Foraging areas were closest to the colony during *Incubation* (1172.20 ± 62.56 km, n = 72), when core foraging areas extended to the APF (62°S) between 120° to 160°E. Birds travelled furthest during *Late-chick rearing* (2114.16 ± 80.53 km, n = 43), when the core foraging areas extended further to the west to 100°E and south to 67°S. Core foraging zones extended to the

Antarctic Zone (AZ) (up to 64°S, 1566.78 ± 53.30 km, n = 66) during the *Early-chick rearing* stage when chicks were small, while during *Pre-laying*, the birds foraged within the APF above 60°S to between 150° - 100°E (1379.31 ± 96.55 km, n = 44).

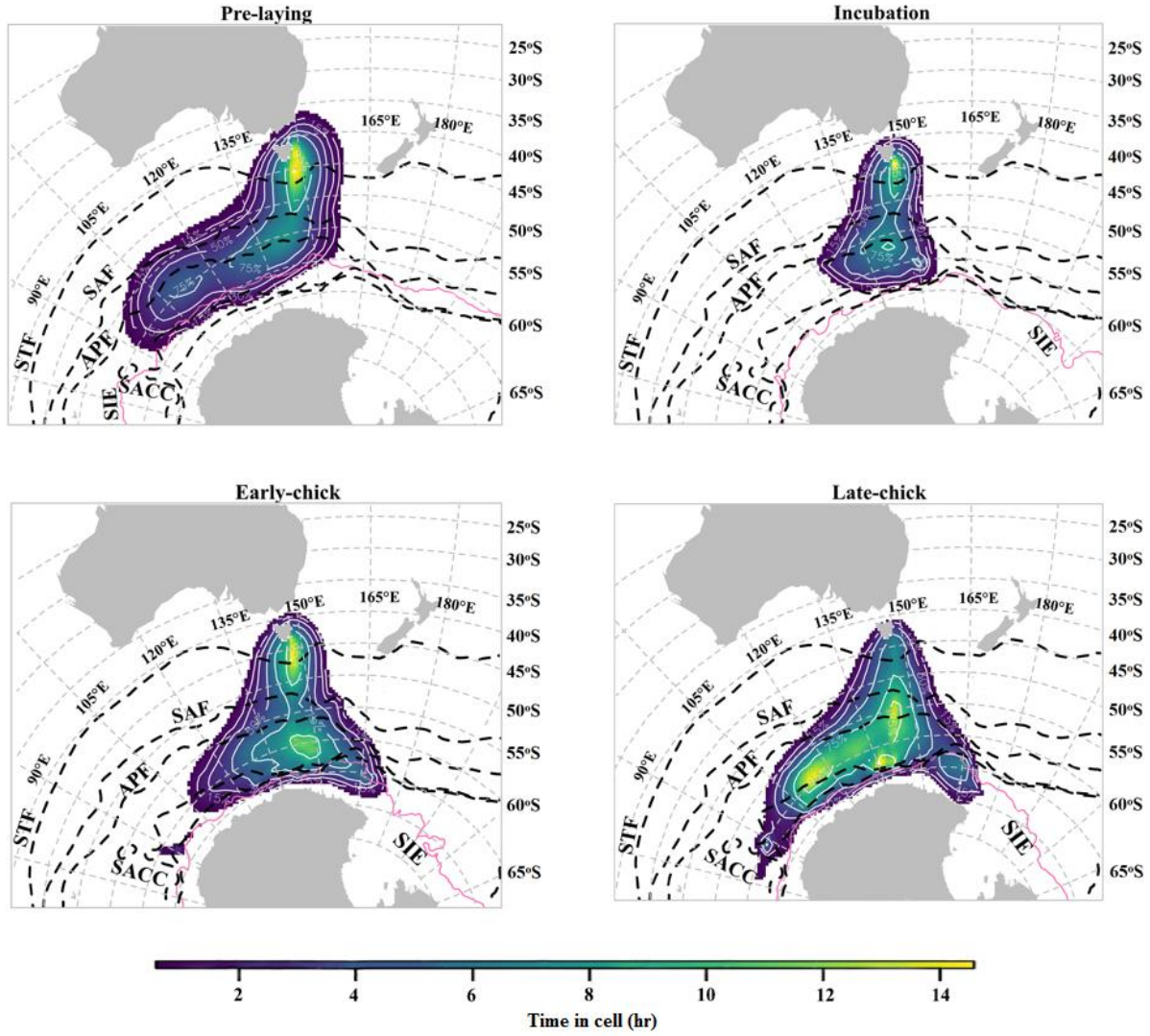


Figure 4.1. Location of core foraging areas of short-tailed shearwaters from Wedge Island (2010 - 2014) during the *Pre-laying* (n = 48), *Incubation* (n = 72), *Early-chick rearing* (n = 66) and *Late-chick rearing* (n = 43) stages of the breeding season. STF = Sub-Tropical Front, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front, SACC = Southern Antarctic Circumpolar Current. SIE = Sea Ice Extent (presented by pink line), for each stage of the breeding season, averages for 2010 - 2014 are presented.

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Distance travelled and links with the SAM

Both the SAM and stage, plus the interaction between them were included in the best model explaining the distance to core foraging areas (Table 4.2a). The SAM strongly influenced the distance to core foraging areas during both the *Pre-laying* and *Late-chick rearing* stages (Figure 4.2). In years when the SAM was negative during *Pre-laying*, birds travelled on average 1848.4 ± 308 km to reach their core foraging areas, whereas when the SAM was positive birds only travelled on average 719.5 ± 346 km. During the *Late-chick rearing* stage, the negative SAM phase also corresponded with increased distance to core foraging areas; 2590.4 ± 558 km compared to 2007.7 ± 414 km when the SAM was positive. There was also a slightly positive relationship between the SAM and distance in the *Incubation* phase 1118.02 ± 231 km compared to 1290.1 ± 211.5 km when the SAM was positive, but the SAM had little effect during *Early-chick rearing* when birds on average travelled 1482.09 ± 153.8 km compared to 1536.9 ± 163.5 km when the SAM was positive.

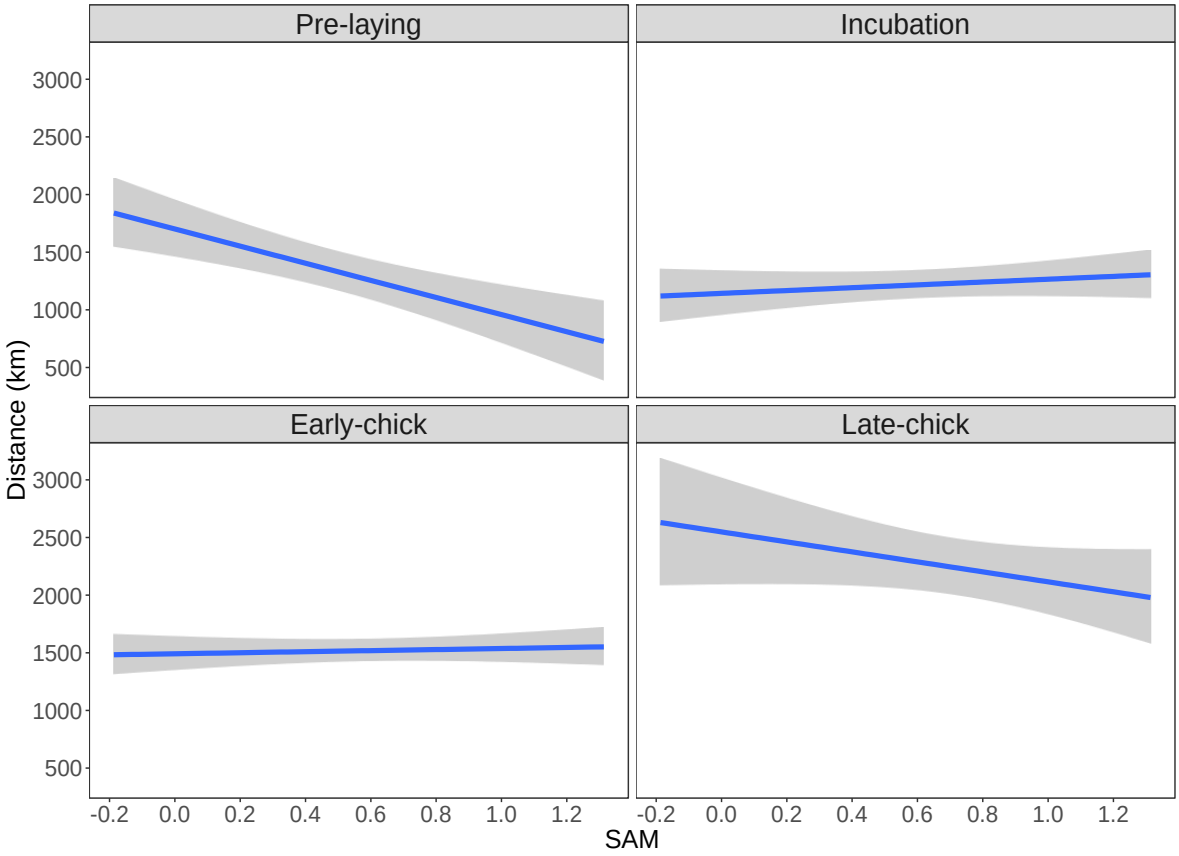

Figure 4.2. The mean distance to core foraging areas of tracked short-tailed shearwaters from Wedge Island (2010 - 2014) during the *Pre-laying*, *Incubation*, *Early-chick rearing*, and *Late-chick rearing* stages in relation to the SAM. Grey shading indicates 95% confidence intervals.

Table 4.2. Linear Mixed Effects Model results for determining:
(a) distance travelled to core foraging areas; and (b) proportion of the day wet (*pwet)*

Candidate models	AIC_C	cAIC	LogLik	ΔAIC_C	wAIC	R^2_m	R^2_c
(a)							
SAM							
1. stage + SAM stage:SAM	-	3482.2	-1719.8	0	0.99	0.35	0.39
2. stage + SAM	-	3497.8	-1733.8	16	<.001	0.30	0.30
3. null	-	3570.1	-1773.9	88	<.001	0.00	0.03
4.SAM	-	3572.2	-1774.9	90	<.001	0.00	0.03
5. stage	-	3572.2	-1774.9	90	<.001	0.00	0.04
(b)							
SAM							
1. stage*SAM	13625	-	-6801.5	0	1	0.04	0.24
2. null	13797.9	-	-6896.0	173.0	<.0001	0.00	0.30

SAM = Southern Annular Mode

The top ranked model is in bold. cAIC, Conditional Akaike's Information Criterion; LogLik, Log Likelihood, ΔAIC_C is the difference in AIC of the models to the best fitting model; wAIC, indicates the probability of the best model. Bird ID was included as the random effect for each model. R^2_m marginal coefficient of determination (values indicate variance of fixed effects) and R^2_c conditional coefficient of determination (variance explained by the fixed and random effects).

Foraging Activity

Overall, the region where birds spent the most time in the water (*pwet*) was situated south of Wedge Island; this area extended from the SAZ (50°S) between 110° to 155°E to the south of the APF (66°S) between 65° to 170°E (Appendix 4.2). In addition, in all stages, birds also spent a large proportion of the day (0.4 – 0.7 *pwet*) in southern Tasmanian waters, which varied between stages in both proportion and location (Figure 4.3). During the *Pre-laying* stage, the highest *pwet* occurred primarily between 70° to 150°E and 50° to 55°S between the SAF and just south of the APF. In comparison, the distribution of foraging activity was constrained between 100° to 155°E but extended further south to 63°S during *Incubation*. The highest *pwet* shifted to below the APF during the *Early-chick rearing* and *Late-chick rearing* stages between 70° to 170°E.

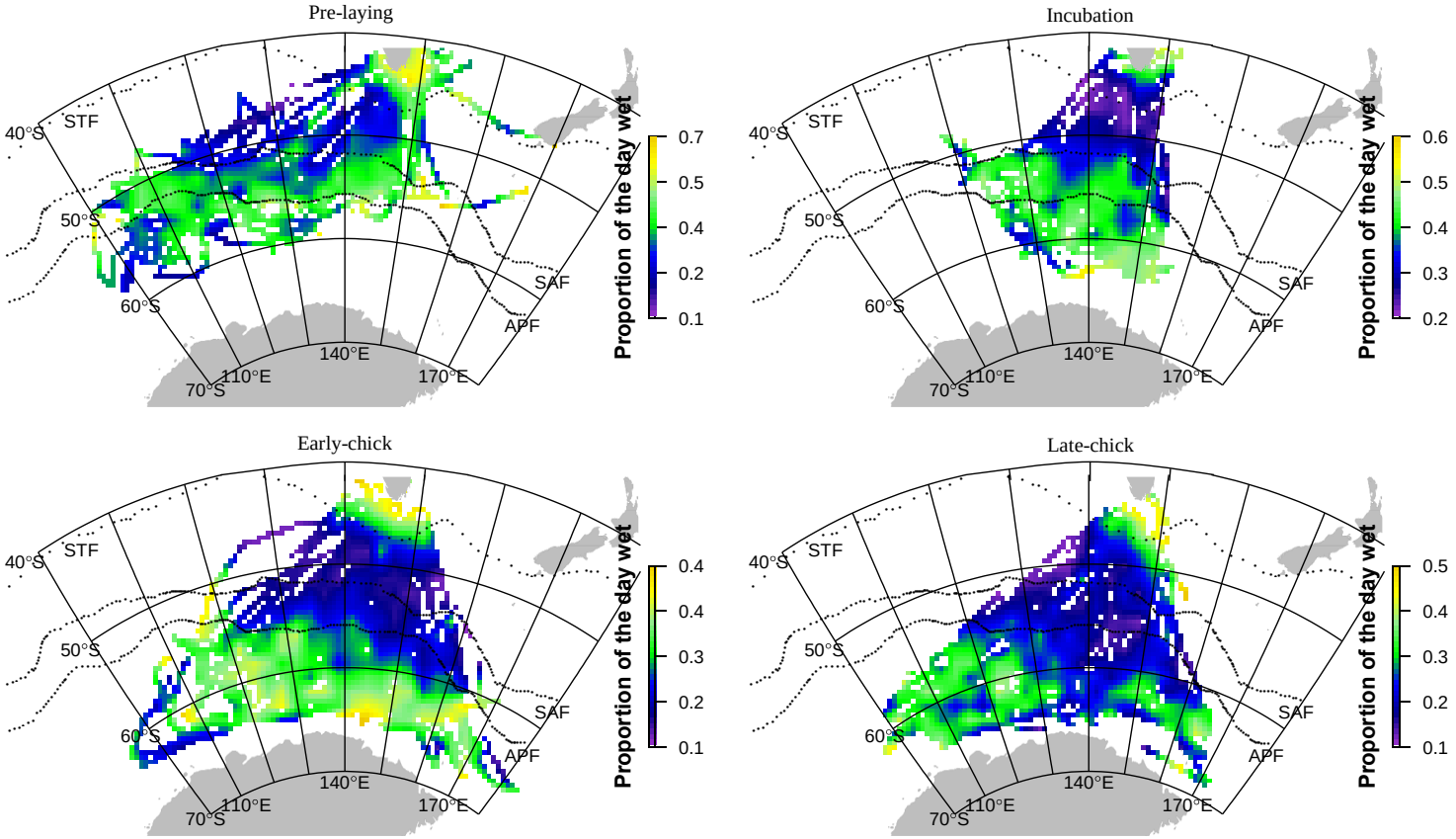

Figure 4.3. The proportion of the day in the water (*pwet*) of breeding short-tailed shearwaters tracked from Wedge Island, 2010 - 2015, overlaid on mean location positions. Right to left: the *Pre-laying* (n = 27), *Incubation* (n = 59), *Early-chick rearing* (n = 50) and *Late-chick rearing* (n = 50) stages. Antarctic Polar Front (AFP), Sub-Antarctic Polar Front (SAF), Sub-Tropical Front (STF).

Foraging activity and the SAM

The model including the *SAM* and *stage* plus their interaction best explained the *pwet* (AIC_C weight = 1, model 1, Table 4.2b). The strongest relationship with the SAM occurred during *Pre-laying*, when birds spent 63% more time in the water when the SAM was positive (Figure 4.4). There was also a slight response to the SAM during the *Late-chick stage*, with birds spending 27% more time in the water when the SAM was high. In the other stages there was no apparent relationship.

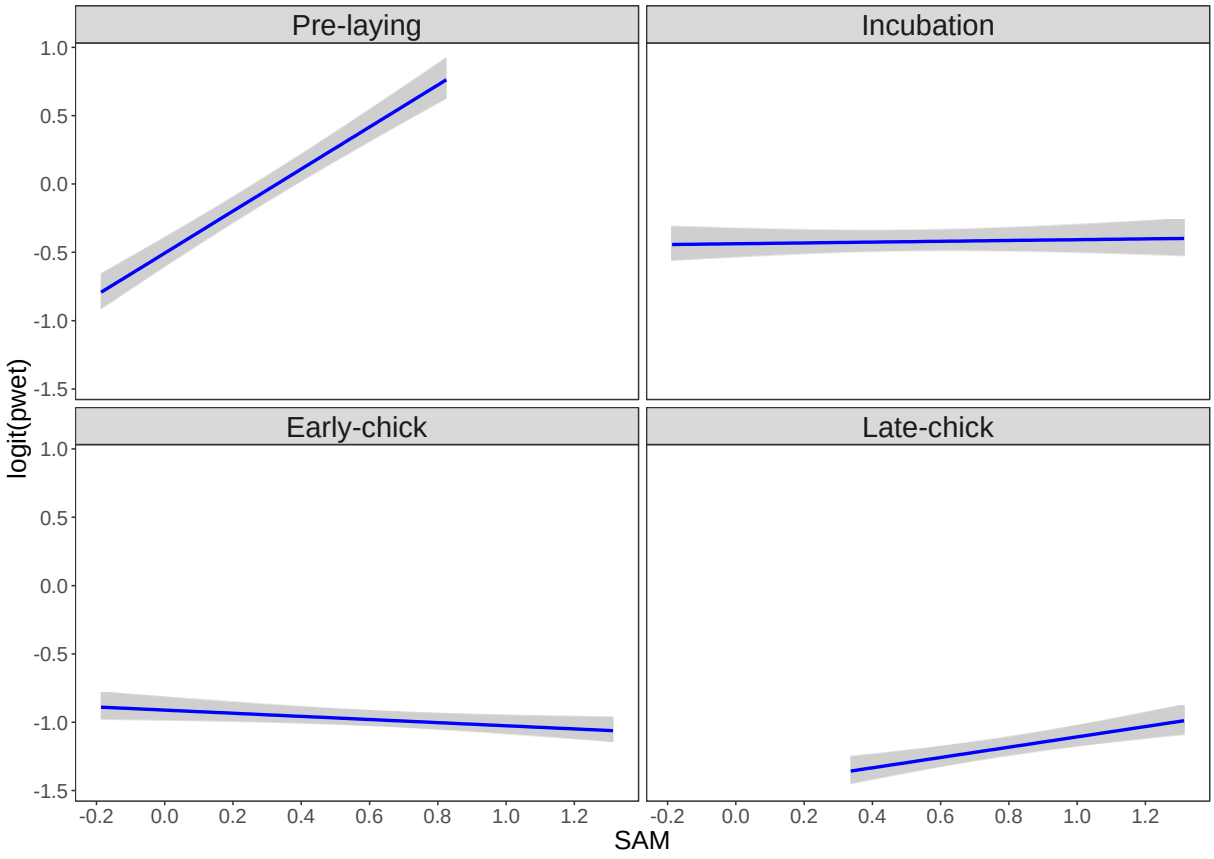

Figure 4.4. The logit scaled proportion of time spent in the water (*pwet*) per day during short-tailed shearwater foraging trips during the *Pre-laying*, *Incubation*, *Early-chick rearing* and *Late-chick rearing* stages in relation to the SAM. 95% confidence interval is indicated by the grey shading.

Short-trip foraging parameters

A total of 12 GPS tracks (2014, n = 3, 2015, n = 9) provided 3154 at-sea position estimates during short, local foraging trips. Six of the 10 units deployed in 2014, were recovered after one day, but three of these failed to record data. A further three birds presumably undertook a long-foraging trip after tag deployment and were subsequently recaptured 1 to 4 weeks after tag deployment during which time they had lost their tags. Ten of the 14 tags deployed in 2015 were recovered. Of these, one bird did not leave its burrow for 2 days after the tag was deployed. By this time the devices' batteries had expired so it did not collect data at sea. Typically, the birds departed the colony prior to sunrise, and spent on average 16 hours foraging within the shallow waters (35 - 80 m) of the continental shelf between 42° - 43°S and 147° - 149°E (Figure 4.5). Birds were recaptured at the colony 1 to 4 hours after sunset. The mean maximum distance travelled from the colony was 42.2 ± 5.5 km (range 19.1 - 83.4 km) and the mean total distance travelled per foraging trip was 207.2 ± 27.1 km (Table 4.3). Flight speed varied throughout the trip, averaging 13.6 ± 1.7 kmh^{-1}, with a maximum speed of 79.6 kmh^{-1}. Overall, birds foraged to the southeast of the colony (mean bearing, 121° ± 20.2°); however, birds also foraged to the north of the Wedge Island, over inshore waters.

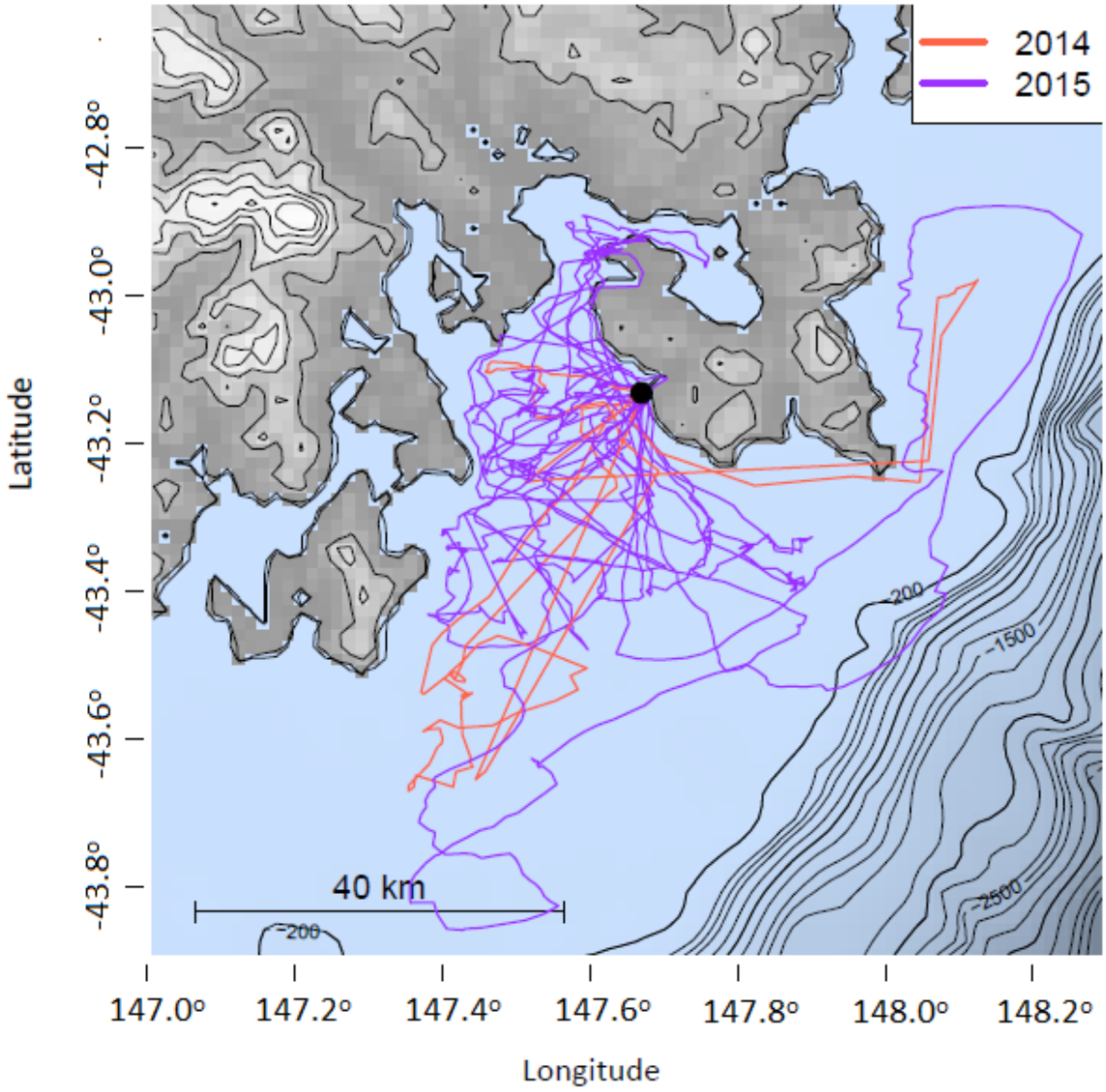

Figure 4.5. Short foraging trips undertaken by 12 short-tailed shearwaters from Wedge Island (2014 – 2015), during the chick-rearing stages. Tracks from 2014 are red (n = 3) and tracks from 2015 are purple (n = 9). Bathymetric contour lines and depth (m) are depicted.

Table 4.3. Short-trip foraging characteristics, including trip duration (hr), total and maximum distance from the colony (km), mean outward bearing (º), mean and maximum horizontal speed (kmh^{-1}) of 12 GPS equipped short-tailed shearwaters during the chick-rearing phase, at Wedge Island (2014 - 2015).

Bird ID	Year	Trip duration (hrs)	Total distance travelled (km)	Maximum distance from colony (km)	Outward bearing from colony (°)	Mean horizontal speed (km/h^{-1})	Maximum horizontal speed (km/h^{-1})
116134	2014	22.1	164.5	40.8	209	20.2	79.6
103635	2014	15.2	206.9	65.0	33	18.0	47.0
116247	2014	16.2	168.7	60.9	101	11.9	61.1
117240	2015	16.5	271.0	42.8	122	14.1	59.6
102779	2015	16.3	142.0	42.9	32	8.2	51.8
102263	2015	16.1	67.2	20.0	50	4.5	41.6
116915	2015	16.5	437.4	83.4	137	24.8	72.7
117230	2015	16.3	127.3	19.1	80	7.4	48.6
117950	2015	15.3	165.4	26.6	83	10.0	61.3
115359	2015	21.4	231.2	34.1	220	10.6	71.9
104193	2015	15.0	261.8	30.4	206	16.8	66.2
115360	2015	14.5	242.7	40.7	188	16.6	58.7
Mean ± SD		16.8 ± 0.8	207.2 ± 27.1	42.2 ± 5.5	121 ± 20.2	13.6 ± 1.7	60 ± 3.3

Relationship between breeding parameters, the SAM and local SST

The number of birds breeding in the survey quadrats varied considerably over the course of the 12 year study ($F_{10} = 10.76$, $P < 0.001$) with a low of 102 in 2008 to a high of 211 in 2014 (Figure 4.6). Breeding success also showed considerable variability among years ($F_{11} = 17.09$, $P < 0.001$) from 19% in 2013 to 83% in 2012 (Figure 4.6). None of the proxies used to indicate prey availability, explained the observed variability in the number of birds that bred (PDO, local SST, Chl *a* and the SAM). Environmental proxies also did not explain the recorded variability in breeding success (local SST, Chl *a* and the SAM) (Table 4.4). In contrast, both local SST and the SAM influenced chick fledging mass (Figure 4.7). Chicks were on average 45 ± 45 g and 26 ± 54 g heavier when the SAM was negative and SST was cooler respectively.

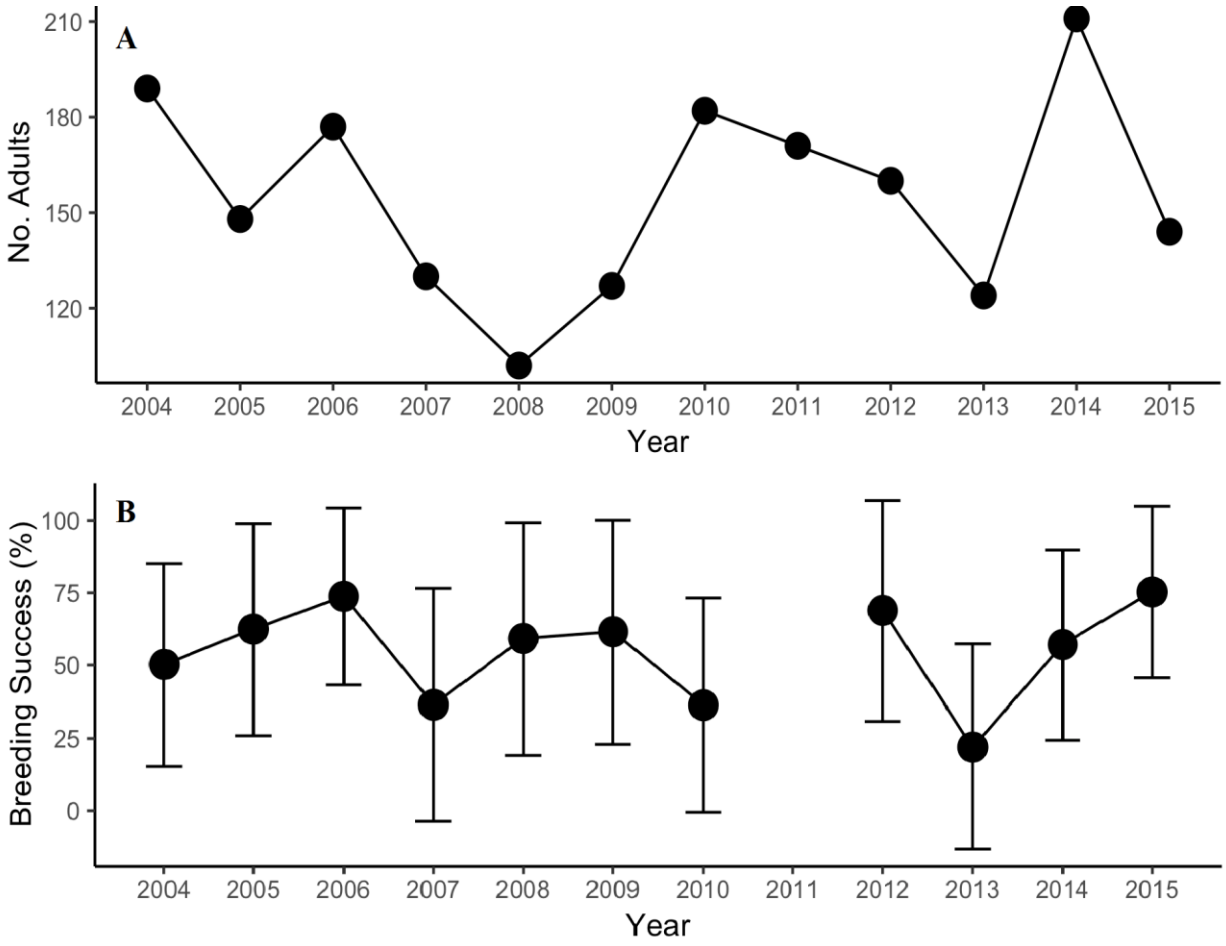

Figure 4.6. Top panel: the total number of adults (with an egg) detected in burrows along set transects at Wedge Island, each December (2004 - 2015). Bottom panel: breeding success (%); the proportion of chicks successfully raised from the number of eggs laid (mean, 95% CI), at Wedge Island, 2004 - 2015, excluding 2011.

Table 4.4. Linear regression model results for determining the influence of environmental variability on: (a) number of birds breeding in December; (b) breeding success (%); and (c) chick fledging mass (g)

Candidate models	DF	LogLik	AIC_C	ΔAIC	wAIC
(a)					
1. null	**2**	**-58**	**121.4**	**0**	**0.4**
2. Birds ~ Chl *a*	3	-56.9	122.9	1.5	0.2
3. Birds ~ winter PDO	3	-57.4	123.8	2.4	0.1
4. Birds ~ winter SST	3	-57.8	124.6	3.3	0.1
5. Birds ~ winter SAM	3	-57.8	124.7	3.3	0.1
(b)					
1. null	**2**	**-48.5**	**102.6**	**0.0**	**0.6**
2. Breeding success ~ SST	3	-47.8	105.0	2.4	0.2
3. Breeding success ~ summer SAM	3	-48.4	106.3	3.7	0.1
4. Breeding success ~ Chl *a*	3	-48.5	106.4	3.8	0.1
(c)					
1. Chick mass ~ summer SST + summer SAM	**4**	**-3327.7**	**6663.4**	**0.0**	**0.5**
2. Chick mass ~ Chl *a* + summer SST + summer SAM	5	-3327.2	6664.5	1.0	0.3
3. Chick mass ~ Chl *a* + summer SST	4	-3329.7	6667.5	4.1	0.1
4.Chick mass ~ Chl *a*	3	3330.9	6667.9	4.5	0.1

Top models are in bold

winter SAM = Southern Annular Mode (May - November); winter SST& Chl *a* (May - November). summer SAM = Southern Annular Mode (December - March); winter SST & Chl *a* (May - November). winter PDO = Pacific Decadal Oscillation index (May - September)

LogLik, Log Likelihood, ΔAIC_C is the difference in AIC of the models to the best fitting model wAIC, indicates the probability of the best model.

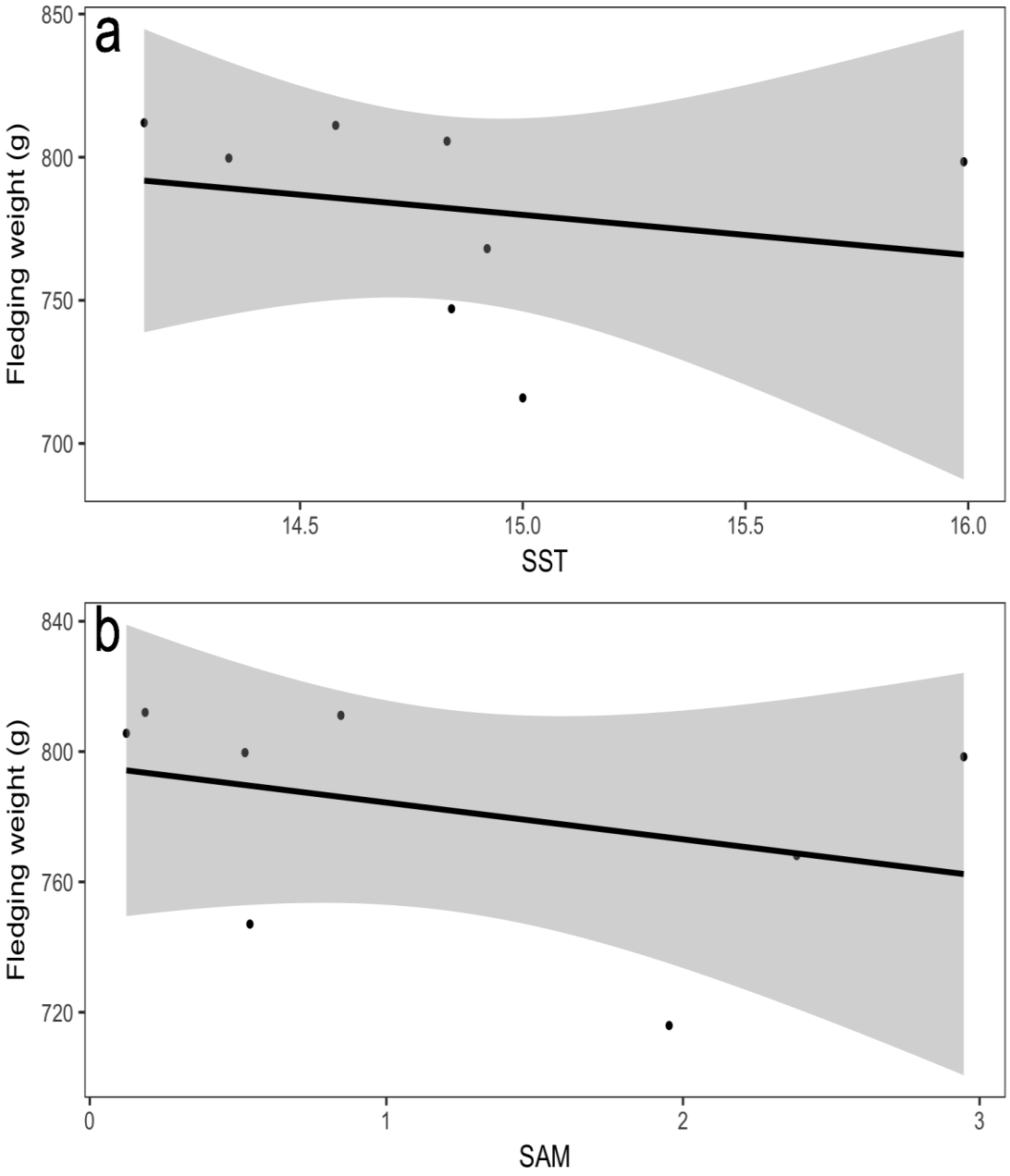

Figure 4.7. Linear regression models for fledging mass of short-tailed shearwater chicks measured at Wedge Island, during the 2005 - 2008, 2010, and 2012 - 2015 breeding seasons in relation to: a) local SST (December - March); and b) the Southern Annular Mode (SAM) (December - March).

Discussion

Short-tailed shearwaters from Wedge Island travelled further and spent less time at the water's surface during long-trips in the *Pre-laying* and *Late-chick rearing* stages when the SAM was negative i.e. when foraging conditions were relatively poor in the Antarctic. However, neither local environmental conditions surrounding the colony, the SAM nor the PDO influenced the number of adults breeding or breeding success. Only chick mass prior to fledging was influenced by local SST and the SAM. This indicates that a complex interplay between the environment, top-down pressures and the life-history of this long-lived species may act to regulate breeding participation and breeding success.

Foraging distribution during long-trips

During long-trips the core foraging areas extended from the SAZ to the AZ, 40°S to 67°S, and ranged from 90°E to 170°E. This region has previously been identified as an important foraging area for a number of marine predators (Nicol et al., 2000), including short-tailed (Berlincourt and Arnould, 2015, Einoder et al., 2011) and sooty shearwaters (*Ardenna griseus*) (Shaffer et al., 2009). The AZ is relatively productive compared to the other Southern Ocean zones due to higher levels of silicic acid, nitrate and iron (Zentara and Kamykowski, 1981), which promotes higher concentrations of primary production (Iida and Odate, 2014, Sokolov, 2008). Short-tailed shearwaters most likely use this region during self-provisioning trips to both reduce competition surrounding the colony (Ashmole, 1963), and to take advantage of the predictably higher productivity in the AZ zone. The region southwest of Wedge Island within the STF (to 46°S) was also a site that the birds spent a large proportion of time on the water, presumably to catch prey for their chicks prior to returning to the colony (Weimerskirch and Cherel, 1998).

Foraging distribution in relation to seasonal sea ice extent

Where seabirds go to find prey can often be related to the timing of peak productivity in foraging areas (Amorim et al., 2009, Haney and McGillivary, 1985). Seabird distribution in the Southern Ocean occurs in predictable seasonal patterns associated with SST changes and sea ice retreat (Commins et al., 2014). When short-tailed shearwaters arrive at their breeding

colonies in early October, the SAZ and AZ are relatively unproductive due to the down-turn in primary productivity associated with reduced light availability over the winter months (Moore and Abbott, 2000). Winter sea ice can extend to 55°S, and does not retreat until October (Taylor et al., 2013), so primary productivity does not peak south of 60°S before December (Smith et al., 2000, Swart et al., 2015). Hence the core foraging area during the *Pre-laying* stage was within the STZ and SAZs (> 60°S). Other features, such as the Antarctic Polar Front and the ACC, are also sites of high productivity due to the convergence of waters bringing nutrients to the surface (Arrigo et al., 2008, Moore and Abbott, 2000). Consequently, following the retreat of the ice edge, short-tailed shearwaters extend their foraging range south to these areas (Woehler et al., 2006), coinciding with the *Late-chick rearing* stage when energy needs are highest.

Interplay between the SAM and foraging behaviour

Short-tailed shearwaters from Wedge Island undertook short foraging trips (~16 hrs) to the shallow neritic waters of the continental shelf of Storm Bay. Short-trips optimise food delivery to chicks by increasing provisioning rates, whereas long-trips serve to maintain the adults body condition (Baduini and Hyrenbach, 2003). For bi-modal foraging to be successful, birds need to maximise the delivery rate of food to their chick, whilst the efficiency of self-foraging at locations distant from the colony must compensate for increased travel time (Welcker et al., 2012, Ydenberg and Davies, 2010). Therefore, the bimodal foraging strategy of short-tailed shearwaters could influence foraging distribution in relation to the SAM in two ways.

Firstly, when the SAM is positive, primary productivity is relatively low in the areas surrounding the colony (Lovenduski and Gruber, 2005). Secondly, at the same time, primary productivity is relatively high in the eastern Antarctic due to up-welling and cooler SST (Lovenduski and Gruber, 2005). Therefore, primary production is enhanced in the areas adults go to during long-trips when the SAM is positive, but foraging conditions surrounding the colony where adults find prey to provision their chick during short-trips could be reduced. Subsequently, we found that when the SAM was positive during *Pre-laying* and *Late-chick rearing*, adults on average travelled 1129 km and 583 km less to find their prey and they spent 63% and 27% more time in the water, per stage, respectively. However, when the SAM was negative, birds travelled further and spent less time on the water. Thus, when SST is warmer in

the regions birds use to self-provision, it is reasonable to expect that prey is scarce; consequently the birds have to travel further to find prey.

Birds travelled less during *Incubation* and *Early-chick rearing* and the distance travelled was not related to the SAM, so adults may not be as food limited during these stages. Incubating an egg requires less energy than feeding a chick (Mallory et al., 2008) and because the incubation shifts of short-tailed shearwaters are long, between 11 - 14 days (Carey, 2011), the partner has sufficient time to regain lost mass. During *Early-chick rearing* adults may be more constrained by the need to return to the colony to feed their small chick, which probably restricts the distance adults can travel from the colony if they are to deliver meals regularly. During *Pre-laying* the bids replenish their energy reserves following the migration from the Northern Hemisphere (Marshall and Serventy, 1956), so the availability of prey will be important if birds are to commence breeding activities (Arizmendi-Mejia et al., 2013, Sandberg and Moore, 1996). As the birds are not tied to colony at this time, they can range more widely. Similarly, the additional energy required to provision a large chick may mean that short-tailed shearwaters are more sensitive to prey scarcity during *Late-chick rearing* (Collins et al., 2016, Harding et al., 2007) as the rising energy requirements of growing chicks typically increases the duration of seabird foraging trips (Adams et al., 1991, Lewis et al., 2004). Therefore, our finding that short-tailed shearwater foraging behaviour was only influenced by the SAM during *Pre-laying* and *Late-chick rearing* is likely associated with higher energy needs at those times. Thus, adults most likely travel further and search more to meet energy requirements when reductions in prey abundance occurs during these stages.

Environmental variability and chick mass

Positive phases of the SAM and warmer SST were correlated with lower short-tailed shearwater chick fledging mass, most likely due to suppressed winds and reduced productivity surrounding the colony (Clementson et al., 1989). Large zooplankton species (*e.g. N. australis*) are absent in the waters surrounding Wedge Island in warm years (Young and Davis, 1992) and Jack mackerel fisheries have collapsed when *N. australis* abundance was low (Harris et al., 1992). Consequently, the benefits of better environmental conditions at higher latitudes when the SAM is positive may be outweighed by poor conditions surrounding the colony.

Einoder et al. (2013) found that energy content was more important than the frequency of meals fed to short-tailed shearwater chicks, i.e. fewer, less frequent meals consisting of high calorie fish from around the colony and high lipid oil delivered following a long-trip resulted in higher fledging mass compared to when the chicks were fed more frequently but with low calorie krill. Short-tailed shearwaters forage bi-modally and this would allow them to adjust the frequency of meals delivered to chicks dependent on the environmental conditions they encounter (Einoder et al., 2013). Nonetheless, our results suggest that the availability of prey surrounding the colony may be an important factor that influences the mass of chicks and this could affect their survival post-fledging.

When chicks fledge with lower weight, they would have reduced reserves to support their migration to the Northern Hemisphere. Reduced weight can also cause immune suppression (Navarro and Gonzalez-Solis, 2007) and could decrease survival post-fledging as chicks divert lipids to feather growth instead of flight (Oka, 1989). McClung et al. (2004) showed that yellow-eyed penguin (*Megadyptes antipodes*) survival post-fledging corresponded positively to fledging weight; further, fairy prions *(Pachyptila turtur)* that fledged with shorter wings in association with an El Nino event had poor survival post fledging (Manno et al., 2014). Considering the long migration short-tailed shearwater fledglings must undertake to the Northern Hemisphere, the energy they have in reserve is likely to influence their capacity to survive the journey. Indeed, short-tailed shearwater fledglings in poor condition strand in large numbers in the waters surrounding Japan (Oka and Maruyama, 1986).

Variability in breeding participation and breeding success

For a migratory species, carry-over effects influencing bird condition from the non-breeding period can affect not only survival during migration but also the capacity of adults to breed (e.g. Fayet et al., 2016b). However, environmental conditions at both local and basin wide scales during the non-breeding stage or just prior to egg laying did not influence the number of birds that bred at Wedge Island. These findings indicate that yet unidentified factors may also contribute to intermittent breeding in short-tailed shearwaters. Measuring the mass of birds as they return from the migration and the development of a model that includes climate

variability, prey availability, breeding participation and bird mass will help to better identify the underlying mechanisms behind the observed variability.

Breeding success was not related to the SAM or local environmental conditions. Rather, on-shore factors could explain the observed variability. On land, seabirds are vulnerable to predators (Phillips et al., 2016). Even native predators, with which seabird populations evolved side-by-side, can have adverse effects on seabird populations (Oro and Furness, 2002), as recent anthropogenic activities can promote the expansion of native predator populations beyond their natural boundaries (Stenhouse and Montevecchi, 1999). Forest ravens (*Corvus tasmanicus*) and native water rats (*Hydromys chrysogaster*), both on Wedge Island, are predators of short-tailed shearwater eggs and chicks (Skira et al., 1986). Raven populations have increased in Australia as a result of urbanisation (Barrett et al., 2003), and have been linked to reduced breeding success of little penguins (*Eudyptula minor*) (Ekanayake et al., 2015). Forest ravens gather on Wedge Island in the hundreds during *Incubation* and *Late-chick rearing* and have been observed eating eggs and preying on chicks in burrows (N. Bool Personal observations), although the extent of this depredation is unmeasured. Fledging success could also be influenced by storm events, as high rainfall can cause burrows to flood (Thompson and Furness, 1991). Summer rainfall explained 48.1% of the variation of short-tailed shearwater chick survival between 1967 to 2003 at Montague Island (Tiller et al., 2013). Further, short-tailed shearwater egg-failure was attributed to heavy rainfall in 1966 and 1970 at Fisher Island (Serventy and Curry, 1984). Depredation of eggs and chicks, coupled with high rainfall in some years, could cause low breeding success at Wedge Island.

Further research is required to determine the mechanisms underlying intermittent breeding and variable breeding success at Wedge Island. This is particularly important as the SAM is predicted to continue to be increasingly positive into the future (Marshall et al., 2013). Estimating the long-term viability of the Wedge Island population will require integrated studies on not just the influence of climate variability but also on the many factors that act on the individual birds.

Acknowledgements

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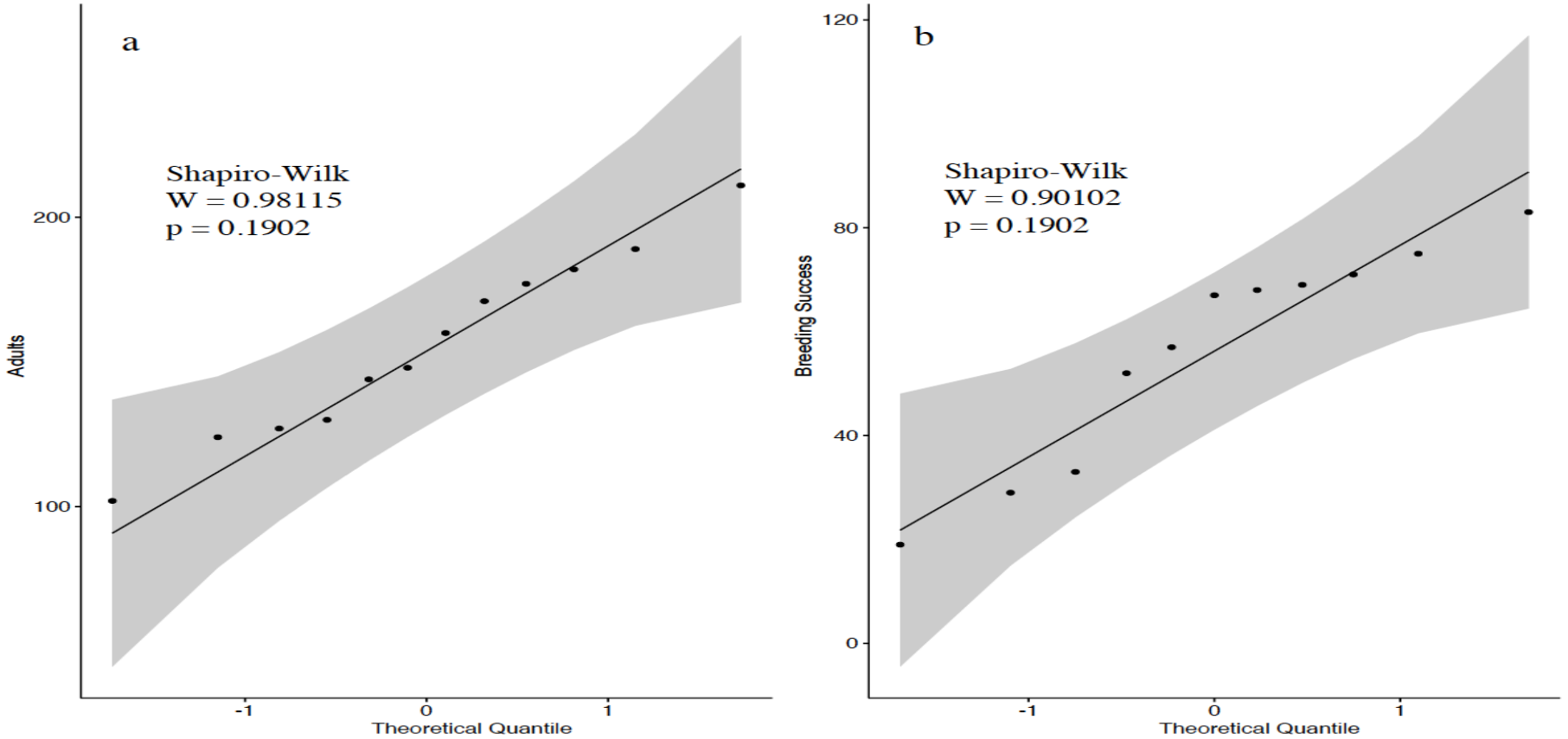
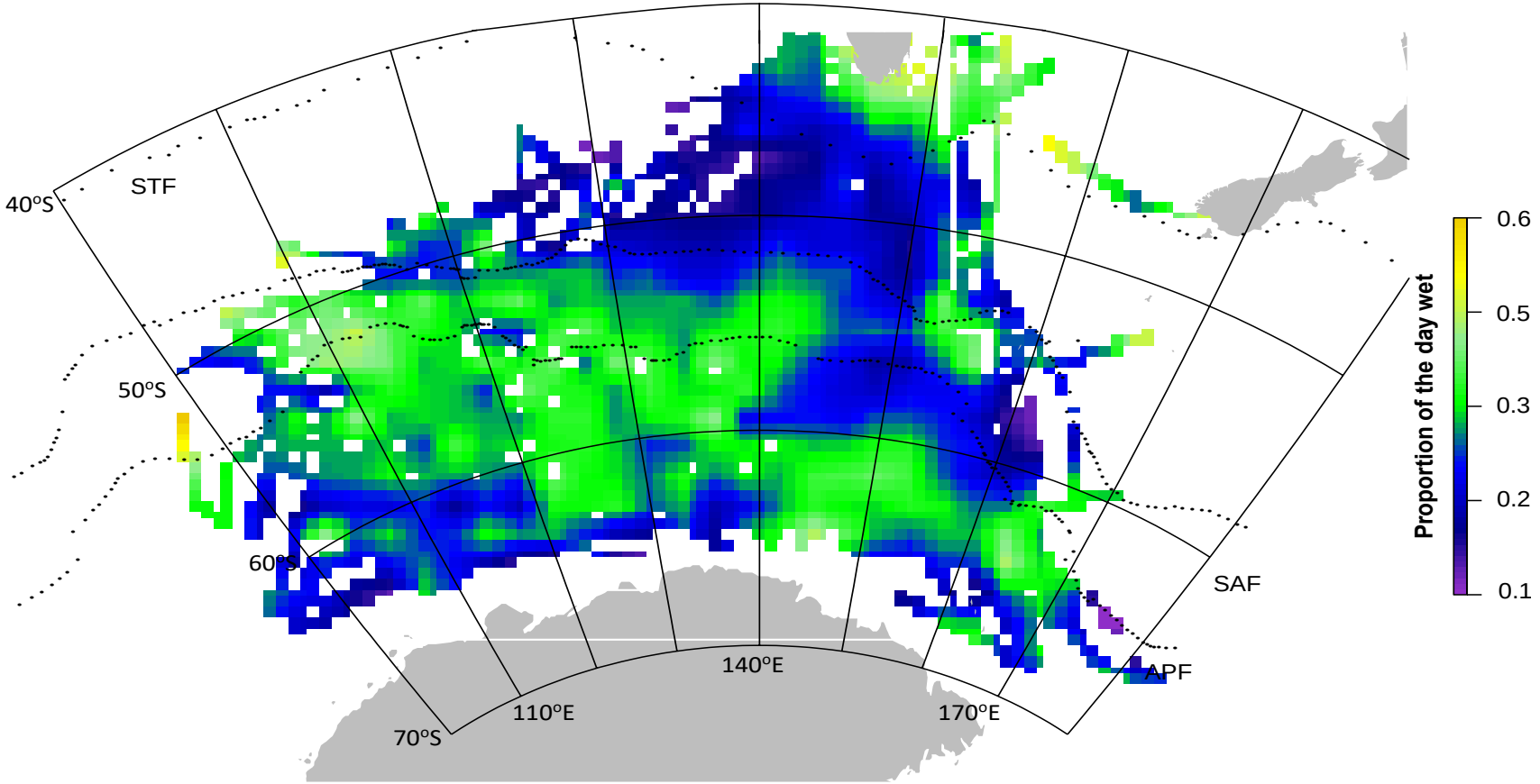
Appendices



Appendix 4.1. Shapiro-Wilk tests for normal distribution of breeding parameter data: a) the proportion of adults that commenced breeding in December at Wedge Island (2004 - 2015); and b) breeding success, the proportion of chicks produced from the number of eggs laid (2004 - 2015 excluding 2011).



Appendix 4.2. Distribution of the proportion of the day in the water (*pwet*) of short-tailed shearwaters (n = 83) tracked from Wedge Island, 2010 - 2014, overlaid on the mean location positions. Antarctic Polar Front (AFP), Sub-Antarctic Polar Front (SAF), Sub-Tropical Front (STF).

CHAPTER 5 GENERAL DISCUSSION

The spatio-temporal foraging distribution and trophic position of animals provide insights into how the complex interplay between life-history traits, top down pressures and environmental variability act to influence individual fitness and population viability (Morales et al., 2010, Suryan et al., 2009). The objectives of this thesis were to investigate the foraging strategies and the trophic position throughout the annual life cycle of a K-selected seabird, the short-tailed shearwater, to understand how resource variability influences reproductive output. The principal findings were: i) during the non-breeding stage birds diverge in their selection of staging areas, but within this adapt their movements in response to changes in environmental conditions; ii) the trophic position of prey consumed during the breeding season to sustain the adult birds does not vary in response to climate variation, rather, birds appear to forage at alternative sites; iii) although this long-lived predator has a flexible bi-modal foraging strategy to maximise the rate of prey delivered to its chick, local prey availability appears to be an important factor determining chick mass; iv) onshore predators and anomalous rainfall events rather than bottom-up factors could affect breeding output.

Foraging behaviour during the non-breeding stage

The foraging decisions made by animals strongly influence the rate at which resources are encountered and this ultimately affects individual fitness (Dill, 1987, McNamara and Houston, 1986, Morris and Davidson, 2000). Within a population individuals can consistently use a subset of the total habitat (i.e. maintain site fidelity) (Bolnick et al., 2003, Ceia and Ramos, 2015). Climate variability can affect the distribution and abundance of food resources among years (e.g. Chavez et al., 2011, Craine et al., 2012, Jonas et al., 2008, Loeb and Santora, 2015). Hence the success of site fidelity can depend on the current availability of resources (Abrahms et al., 2018); nonetheless for long-lived individuals site fidelity is an evolutionarily stable strategy (ESS) because over the long-term repeated use of a site should be equally successful across the population (Hines, 1987). However, if directional climate change continually decreases the profitability of a site, then a high level of fidelity could result in reduced fitness and population viability if enough individuals continue to use increasingly low productive areas (Cooch et al., 1993, Hindell et al., 2017). Therefore,

behavioural plasticity and the selection of alternative sites will become increasingly important if resources are less predictable (Switzer, 1993).

Chapter 2 explored individual selection of foraging sites and behavioural plasticity of short-tailed shearwaters during the non-breeding stage. An important finding was that short-tailed shearwaters returned to sites where the spring bloom would provide a predictable rich source of prey (Hirota and Hasegawa, 1999, Iida and Saitoh, 2007, Sigler et al., 2014, Weimerskirch, 2007). Further, two spatially distinct primary core foraging sites in the North Pacific Ocean were identified, the Sea of Okhotsk/North Pacific Ocean (Western group), and the southeast Bering Sea/North Pacific Ocean (Eastern group). In addition, a subset of birds from across the groups left their core area and moved to the Chukchi Sea toward the end of the non-breeding stage.

Optimal foraging theory specifies that the effort expended whilst searching and handling resources should be balanced by net energy gain, so individuals should select a foraging strategy that will maximise energy gains (Stephens and Krebs, 1986). But when food resources decline and if individuals can no longer 'optimally' balance foraging time with net energy gains in their chosen foraging site, they should 'give up' and search for resources elsewhere (Charnov, 1976). The late season movements by short-tailed shearwaters to the north Bering Sea and Chukchi Sea coincided with declining concentrations of chlorophyll *a* in the Western and Eastern core regions. This suggests that where short-tailed shearwaters forage is coupled with environmental conditions, which is likely associated with the availability of prey at these sites. Regional warming and increasing levels of primary productivity (Arrigo and van Dijken, 2015) are enabling pelagic organisms to extend their range into the Chukchi Sea (Grebmeier et al., 2006b). This probably provides a predictable source of prey (such as large bodied krill), which can be utilised when resources become depleted in the southern Bering and Okhotsk Seas and, as a result, shearwaters are increasingly found in this region (Gall et al., 2017, Hunt et al., 2014, Nishizawa et al., 2017).

Considering that the availability of resources animals use are forecast to become less predictably available as global temperatures rise (Parmesan, 2006, Parmesan and

Yohe, 2003), they will need to adapt in order to persist into the future. Adaptation can occur by shifting the distribution of phenotypes through evolutionary processes (i.e. micro-evolution) (Lavergne et al., 2010, Visser, 2008) and also through physiological and behavioural plasticity (Williams et al., 2008). Short-tailed shearwaters have long-generation times and low fecundity, so the pace of evolutionary adaptation may not match the rate of climate change. However, foraging plasticity appears to be an important tactic that this K-selected species uses to maintain fitness, which could become increasingly important if the distribution and abundance of their resources decline in a rapidly changing environment.

The influence of climate variability on trophic position

Monitoring trophic position over time provides a base from which to assess change in resource availability and how this relates to reproductive parameters and population trajectories. Changes in trophic position that encompass multiple trophic levels indicate broader climate induced alterations of prey composition and abundance and even food-web structure (Kaeriyama et al., 2004, O'Connor et al., 2009, Petchey et al., 1999, Sydeman et al., 2015, Wainright et al., 1993). Identifying these changes is important because the abundance and the quality of prey can determine breeding performance and the successful recruitment of juveniles into the breeding population (Cury et al., 2011, Österblom et al., 2008, Trites et al., 2007).

Chapter 3 examined whether ocean baseline variability influenced nitrogen stable isotope values, which provided insight into the relationship between environmental variability and trophic trends of breeding short-tailed shearwaters when undertaking long foraging trips. Both nitrogen and carbon isotopes vary spatially across the oceans. Nitrogen isotopes in the form of particulate organic matter (POM) (e.g. algae and phytoplankton) vary at the base of the food chain both spatially and temporally (McMahon and McCarthy, 2016, Tamelander et al., 2009, O'Reilly et al., 2002). Likewise, oceanic phytoplankton has lighter $\delta^{13}C$ than inshore plants, and this difference is used to determine onshore versus offshore foraging in marine organisms (Kelly, 2000, Ramos and Gonzalez-Solis, 2012). The observed variability in nitrogen values between the non-breeding and breeding seasons were associated with differences in the baseline concentrations in the North Pacific and Southern Oceans

rather than trophic distinctions (DiFiore et al., 2010, Veit-Kohler et al., 2013). Bulk stable isotope analysis is commonly used to examine the trophic position of a broad range of species (Kelly, 2000). The findings in this thesis add to the growing body of evidence that emphasise the importance of considering baseline isotopes of wide-ranging marine predators.

The Southern Annular Mode (SAM) is a broad-scale climate index of the Southern Ocean (Lovenduski and Gruber, 2005, Thompson and Wallace, 2000), and thus provided an indication of foraging conditions in the regions shearwaters used during long-foraging trips. When the SAM was negative, carbon values indicated that the birds foraged within the sub-Antarctic Zone, and they moved pole-wards when the SAM was positive. There was no relationship with the trophic position of prey and the SAM, suggesting that breeding short-tailed shearwaters deal with changing conditions by modifying where they forage rather than eat lower trophic prey. Nitrogen stable isotope values in this study provided further evidence that suggest that the diet of breeding short-tailed shearwaters contains a large proportion of myctophid fish (Connan et al., 2005), indicating that breeding birds may preferentially select fish that are comparatively higher in energy during this energetically costly stage.

The use of SIA/AA-CSIA in this thesis provided significant insights into long-term trends in the trophic level of prey consumed by adults during long foraging trips. Collecting blood samples from adult birds is relatively easy and is comparatively less invasive than obtaining stomach regurgitates. Nonetheless, monitoring the frequency of meals and the trophic level of the prey fed to chicks will improve our understanding of how important the availability of high calorie local prey is to chick growth and condition and presumably fledgling survival.

Foraging behaviour in response to changes in the Southern Annular Mode

Producing viable offspring requires a substantial investment of energy and time (Reznick, 1985, Shine, 1980, Speakman, 2008). For seabirds, the breeding season is divided into several stages; pairs must procure a nesting site, store energy for reproduction and incubation, and then provision young. These stages require varying levels of energy and consequently seabirds may vary their foraging behaviour in

response to climate fluctuations during these times in contrasting ways (Adams et al., 1991, Lewis et al., 2004, Mallory et al., 2008).

Chapter 4 details the responses of short-tailed shearwaters to climate variability with respect to breeding stage. Foraging behaviour was not affected by climate variability during *Incubation* and *Early-chick* rearing. However, breeding adults travelled more and spent less time in the water when undertaking long-trips during the *Pre-laying* and *Late-chick* rearing stages when the SAM was negative. The energy needs of adults are likely greatest during these stages (Harding et al., 2007), consequently when resources are depleted in the areas birds forage during long-trips, they would need to spend more time looking for prey (Arizmendi-Mejia et al., 2013, Lewis et al., 2004). Although adults travelled further when the SAM was negative, chicks were heavier. Primary productivity would be enhanced in areas surrounding the colony when the SAM is negative, and SST is cooler. This finding suggests that the increased travel costs to adults during self-provisioning trips is offset by the availability of prey surrounding the colony. Short-trip foraging success is an important factor affecting chick mass as this is where a large portion of the calories delivered to chicks is obtained (Einoder et al., 2013).

The finding that chick mass was positively associated with cooler SST and negative SAM could be cause for concern. In recent years, Storm Bay has been influenced by the southwards incursion of the warm waters of the East Australian Current (EAC) (Johnson et al., 2011) and because the SAM has become increasingly positive (Villalba et al., 2012), ocean productivity in this region could decline. During years of warmer SST, the zooplankton and fish that shearwaters catch to feed their chicks are in low abundance in areas surrounding Wedge Island (Harris et al., 1992, Young and Davis, 1992), this is likely to result in chicks receiving less energy. The capacity of adults to produce viable offspring could be reduced in the future and this may decrease long-term recruitment if chick survival post-fledging declines.

Top-down predation

Carry-over effects occur when the state of an individual in one point in its annual cycle is transferred to other stages making overall fitness conditional on prior resource encounter rates (Fretwell, 1972, Harrison et al., 2011, Inger et al., 2010). Therefore, intermittent breeding is a tactic employed by long-lived animals to maximise lifetime reproductive output. Raising young is costly, so individuals may defer reproduction to when conditions are more favourable (Cubaynes et al., 2011, Nur and Sydeman, 1999, Shaw and Levin, 2013, Bull and Shine, 1979). Therefore, it was not surprising that the number of breeding birds varied considerably among years (Chapter 4). Despite evidence for coupling of reproductive effort, output and climate variability in other seabirds (Dunlop et al., 2002, Gremillet and Boulinier, 2009, Hipfner, 2008, Mills et al., 2008), the number of birds breeding and breeding success at Wedge Island were not related to climate variables. The underlying mechanisms associated with intermittent breeding of short-tailed shearwaters remain unclear. There are linkages between pink salmon (*Oncorhynchus gorbuscha*) abundance and short-tailed shearwater body condition and breeding success of resident seabirds in the North Pacific (Springer and van Vliet, 2014, Toge et al., 2011). Further the abundance of short-tailed shearwaters at Montague Island was associated with salmon density in 2005 to 2016 and it also appears that migration wreck events are more likely to occur when pink salmon are in high abundance (Springer et al. 2018). However, a strong relationship was not found between pink salmon abundance and the number of birds that bred at Wedge Island (Springer et al. 2018).

Disentangling the relative roles of top-down and bottom-up forces in the regulation of animal populations remains one of the greatest challenges of ecologists (Hunter and Price, 1992). This is because animal populations are influenced by multiple factors that may interact to impact demographic parameters, including climate mediated resource availability and predation pressures (Caughley, 1994). There is considerable evidence linking climate change to reproductive parameters and demography in seabird populations (e.g. Barbraud and Weimerskirch, 2001, Jenouvrier et al., 2003, Kitaysky et al., 2006, Springer et al., 2007, Sydeman et al., 2001). However, predation of adults and young can also cause population decline (e.g. Boveng et al., 1998, Estes et al., 1998, Jones et al., 2008). Few studies have addressed the

cumulative effects of climate variability and predation on marine predator populations. However, Schwarz et al. (2013), discovered that even though the Antarctic Oscillation (AAO) influences demographic rates of adult Antarctic fur seals (*Arctocephalus gazella*), leopard seal (*Hydrurga leptonyx*) predation is driving localised population decline. The extent of predation at Wedge Island is unknown, but it is probable that forest ravens (*Corvus tasmanicus*) and water rats (*Hydromys chrysogaster*) (Ekanayake et al., 2015) and anomalous rainfall events (Tiller et al., 2013) could reduce breeding success in some years.

Flexibility in foraging behaviour

Although marine resources are patchily distributed and vary on multiple spatial and temporal scales (Weimerskirch, 2007, Welcker et al., 2009), it appears that short-tailed shearwaters return to foraging sites such as ocean fronts, where prey can be found more predictably during both the breeding and non-breeding stages (Chapter 2 & Chapter 4). The findings of this study indicate that when individuals fail to acquire enough energy in the core foraging areas, it prompts birds to undertake a broader search for resources. The overall core foraging area of breeding birds extended from Wedge Island (43°S) to 69°S between 80°E to 170°E. Whereas, the foraging range of failed breeders from Wedge Island (n = 12, data not previously presented), was considerably greater than that of breeding birds. Failed birds dispersed westwards from the colony up to 18°W some 4027 ± 1169 km (range 1591 - 5752 km) beyond the core breeding foraging area (80°E) (Figure 5.1). These birds were no longer constrained by the need to return to the colony; so, rather than forage in the vicinity of breeding birds and presumably where resource availability was reduced, they moved westwards.

The distribution of failed birds broadly overlapped with where the highest densities of Antarctic krill (*Euphausia superba*) occurs in the Southern Ocean; between 180°E and 60°W (Figure 5.2) (Atkinson et al., 2008). The fish that short-tailed shearwaters eat are consumers of zooplankton (Cherel et al., 2010) and higher densities of these fish may also coincide where krill is abundant. Further, short-tailed shearwaters consume a wide variety of prey including copepods, krill and fish during the non-breeding season (Baduini et al., 2006). So it is possible that failed breeders travel to

this region where krill is abundant and consume larger quantities of krill than when they are provisioning chicks.

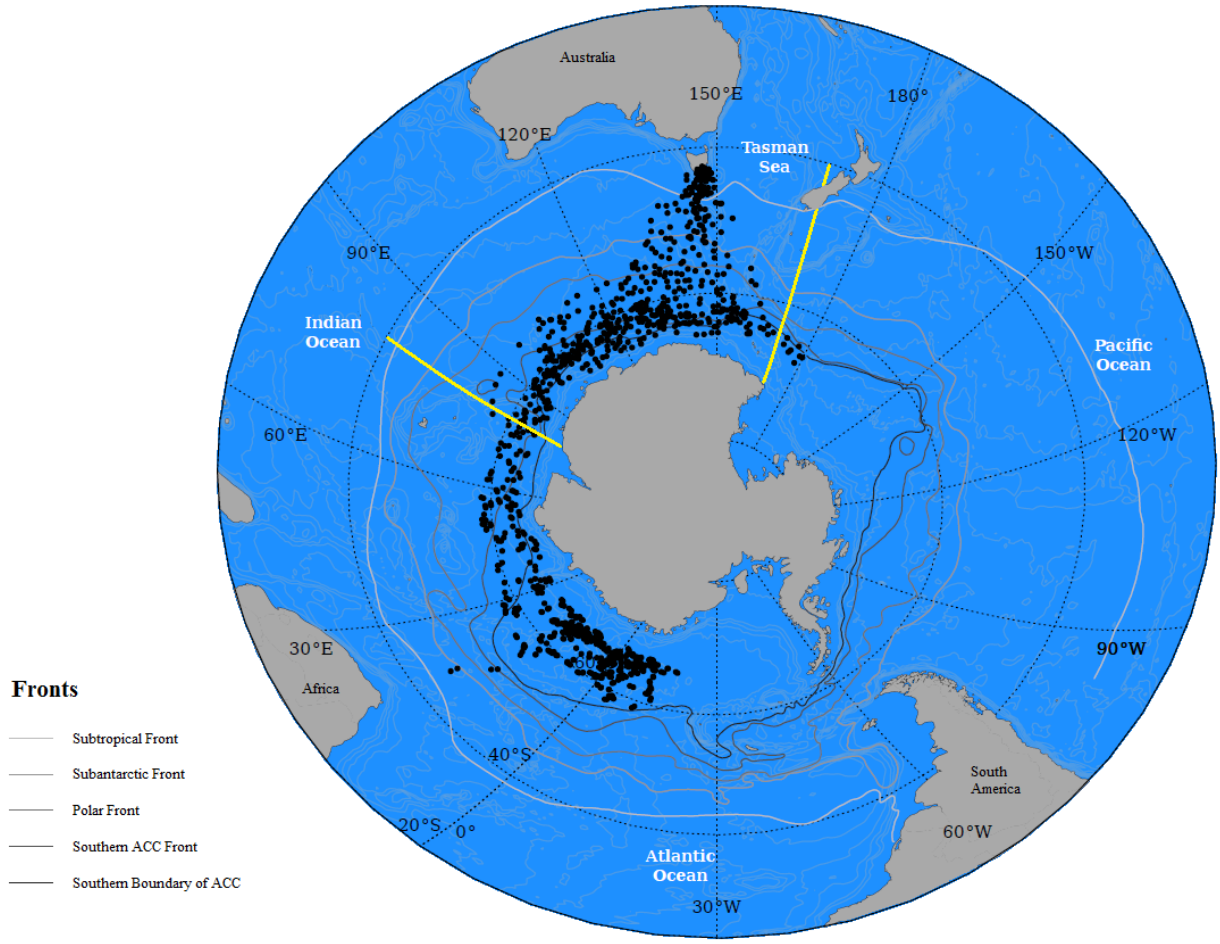


Figure 5.1. The foraging distribution of failed breeders (2012 – 2015, n = 12) from Wedge Island. The yellow lines denote the core foraging region used by breeding birds.

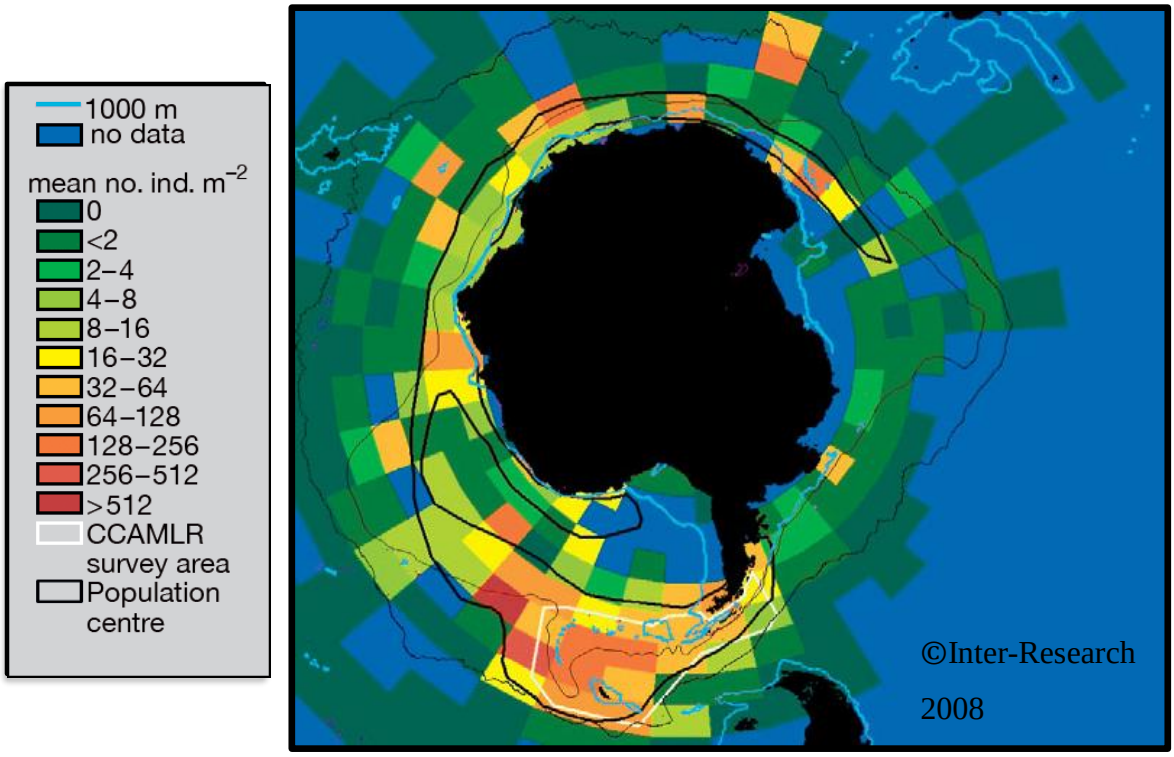


Figure 5.2. Sourced from Atkinson et al. (2008). The circumpolar distribution of krill (*Euphausia superba*) based on standardised data from KRILLBASE (8789 stations including those north of the Antarctic Polar Front, APF). The data are plotted as arithmetic mean krill densities (ind. m^{-2}) of all stations within each 3° latitude by 9° longitude grid cell. Antarctic Polar fronts are denoted by black lines. The orientation of the map presented here is modified from the original publication. Instead the map orientation is centred at ~150°E to highlight the overlap of failed breeders from Wedge Island and krill density.

Life-history traits and climate change; can short-tailed shearwaters adapt?

It is evident that animal species will vary in their capacity to adapt to directional climate change (Bronson, 2009, Parmesan, 2006). Those species with less flexible life-history strategies are likely to be more vulnerable to protracted change in the distribution and availability of resources (Clavel et al., 2011, Croxall, 1992, Forcada et al., 2008, Morrison and Hero, 2003). For example, some high latitude amphibian species have declined in association with increasing temperatures, potentially because of a number of life-history traits such as low fecundity and delayed maturity (Morrison and Hero, 2003). In contrast, some species of seabirds have had positive responses to change in their environments, such as the Audubon's shearwater (*Puffinus lherminieri*); warming temperatures promote higher chlorophyll *a*

concentrations and so the population is growing in association with increasing SST (Precheur et al., 2016). Additionally, some penguin species are projected to extend their range pole-wards as more ice-free habitat becomes available (LaRue et al., 2013, Peron et al., 2012), whereas ice-dependent seals, polar bears and penguin populations that rely on snow and ice for breeding or hunting are predicted to precipitously decline if warming continues and if they fail to successfully use other habitats (Barbraud and Weimerskirch, 2001, Hezel et al., 2012, Stirling and Derocher, 2012, Womble et al., 2010).

Seabirds that are long-lived, wide ranging and which occupy a broad dietary niche may possess behavioural and life-history mechanisms that enable adaptation to a changing climate more quickly than through evolutionary pathways alone (Dall et al., 2012, Teitelbaum et al., 2016). Birds can improve their foraging ability and breeding success through experience (Peron and Gremillet, 2013, Riotte-Lambert and Weimerskirch, 2013, Votier et al., 2017), and this could lead to the development of alternate foraging and diet specialisations and to range extensions within the time-scale of an individual's life-span (Sutter and Kawecki, 2009, Teitelbaum et al., 2016). Behavioural adjustments, however, will only provide benefits if new habitats are within the foraging range of the colony and if the prey found there meets the energy requirements for reproduction and survival.

Trophic status

Changing ecosystem dynamics can restructure community assemblages, and directly affect seabird diet (Davoren and Montevecchi, 2003, Grecian et al., 2016a, Hatch, 2013). For example, the trophic position of the flesh-footed shearwater (*Puffinus carneipes*) declined over a 75-year period concurrent with a two-fold increase in dietary niche (i.e. the diet was at a lower trophic level overall, but with increased variability). This change may be contributing to the decline of this species (Bond and Lavers, 2014). However, downward trophic shifts do not always have adverse consequences for population viability. Contrary to concerns that the cause of population decline of eastern-rock hopper penguins (*Eudyptes chrysocome filholi*), was a consequence of ecosystem changes and a lower trophic position, these seabirds

performed better when their diet was dominated by zooplankton (Morrison et al., 2014).

In the case of the short-tailed shearwater, the trophic position of birds undertaking long-foraging trips during the breeding stage remained constant in years of contrasting SAM. Although short-tailed shearwaters can modify their diet dependent on the resources available to them (Baduini et al., 2006), their trophic position did not shift during the seven-year period of this study (Chapter 3). The quality of prey available during the breeding season may be an important factor involved in chick fledging mass. However, there are three important points to note: 1) the duration of this study may not be sufficient to detect a long-term change in trophic position (Bond and Lavers, 2014), but the use of museum specimens or semi-fossilised material may help ascertain whether any long-term shifts have occurred in relation to climate trends (Emslie and Patterson, 2007, Ostrom et al., 2017); 2) more subtle changes in trophic position between years may not have been detectable with the use of SIA; and 3) chick diet was not assessed in this study. Previous work indicates that adults select a wide range of prey to provision chicks (Skira, 1986) and the quality of prey influences chick condition (Einoder et al., 2013), hence trophic shifts in chick diet among years may occur more readily and could better explain breeding performance than adult trophic position alone.

Range expansion

In response to long-term changes in the distribution of their resources, seabirds could expand their foraging range to encompass a wider region in which to search for prey (Bowler and Benton, 2005, Gremillet and Boulinier, 2009). However, not all species will have the capacity to rapidly extend their foraging range. For example, the Kerguelen shag (*Phalacrocorax verrucosus*) is an adept diver but has limited flight capabilities and often rests on the surface between bouts of flying (Watanabe et al., 2011), thus it is unlikely to substantially extend its foraging range during breeding or quickly establish new distant colonies. Even those species that are capable of swift extended flight ranges will remain constrained by the need to return to land-based nests when breeding (Stephens and Krebs, 1986). Consequently, dispersing to new habitats, whilst maintaining affinity to the natal colony for breeding, may for some

seabirds be a more viable option during the non-breeding stage. For example, the analysis of carbon in feathers of Antarctic prions (*Pachyptila desolata*) revealed a pole-wards range shift during the non-breeding season, perhaps coinciding with more favourable conditions in high latitudes as a result of recent atmospheric forcing (Grecian et al., 2016b).

Although some seabirds show strong natal colony fidelity, young birds that have been forced to leave their natal colony due to prey shortages may establish new breeding colonies in closer proximity to more profitable prey patches. For example, displaced tropical seabirds in Western Australia established new southern colonies during El Nino events (Dunlop, 2009). Similarly, several species of seabirds from the Western Cape Province in South Africa extended their range eastwards in response to the long-term shift of their principal prey, sardine (*Sardinops sagax*) (Crawford et al., 2008). Establishing new colonies within closer proximity to their prey's populations would have prevented extended commutes when provisioning young.

Short-tailed shearwaters can modify their foraging distribution zone throughout the annual cycle (Chapter 2). Range expansions may prove beneficial if more abundant resources can be located in the new areas. However, the distance breeding birds can roam will be limited by the need to return to the colony and because there appears to be low rates of inter-colony dispersal, range extension of breeding birds is likely to remain restricted (Bradley et al., 1991), particularly as there are few suitable landmasses south of the current breeding distribution of short-tailed shearwaters.

Short-tailed shearwater population trends

The lack of data on long-term population trends makes it difficult to assess the current status of the short-tailed shearwater. With a generation time of 18 years (BirdLife-International, 2017) and the presence of hundreds of colonies distributed over thousands of kilometres, an accurate assessment of the conservation status of the short-tailed shearwater will require an extensive and long-term commitment. There is certainly proof that there have been long-term declines at some colonies. In northern-central Bass Strait, the number of breeding burrows declined by 30% (-1.4% per annum) between 1980 and 2011 (Schumann et al., 2014). The number of chicks

produced at Montague Island fell by 50% in the 1980s, and total chick production declined at around -4% y^{-1} during 2000 to 2015 and the number of eggs laid at the Furneaux Islands decreased by -2.1% y^{-1} between 1997 to 2015 (Springer et al., 2018b). The overall trend in the number of birds breeding at Wedge Island was relatively stable (r^2=0.002). However, the short-time series precludes any meaningful assessments of the status of the population.

Intermittent breeding or nest abandonment in favour of both long-term survival and lifetime reproductive output is a tactic used by short-tailed shearwaters to deal with short-term climate anomalies. Climate change in conjunction with top down pressures including predators, and a commercial and recreational harvest, are likely reducing population recruitment, which may have contributed to some of the observed declines (Schumann et al., 2014, Springer et al., 2018a). The relatively recent closures of most drift net fisheries in the North Pacific have cut the incidence of by-catch of short-tailed shearwaters, thus mitigating at least one potential source of decline (Uhlmann et al., 2005). The species is long-lived, wide-ranging, has an extended chick rearing period and can defer breeding to times of greater food abundance, all traits that would have contributed to its overall success and high abundance. Further, bi-modal foraging is an important adaptive tactic that this species uses to sustain energy delivery to chicks in a heterogeneous environment, although current climate trends may limit the effectiveness of this strategy. Overall short-tailed shearwaters may not be as sensitive to environmental change compared to species with less flexible life-history traits and restricted ranges. It is likely that short-tailed shearwaters will persist into the future but with a population smaller in magnitude because of declining habitat carrying capacity. The recorded declines and the uncertainty surrounding the mechanisms underpinning intermittent breeding and breeding success signal a need to bridge the current gaps in knowledge. Further, a better estimate of the population status of short-tailed shearwaters is long over-due. Such insights will provide additional understanding of the population resilience of this predator of meso-pelagic species into the future.

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